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DISPERSION AND MOBILITY IN A LOCAL POPULATION OF SPRUCE GROUSE
(CANACHITES CANADENSIS FRANKLINII)

BY

© PATRICK WALTER HERZOG

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Dispersion and Mobility in a Local Population of Spruce Grouse (*Canachites canadensis franklinii*)", submitted by Patrick Walter Herzog in partial fulfillment of the requirements for the degree of Master of Science.

ABSTRACT

An intensive study of movements and the resulting spacing in a local population of Franklin's spruce grouse (*Canachites canadensis franklinii)* was conducted in southwestern Alberta from April through September 1974 and February through November 1975. Movements were monitored using radio-telemetry. Major emphasis was placed on the female cohort of the population in an attempt to relate the dispersion of residents to spring dispersal of juveniles.

Those adults and juveniles of both sexes that successfully entered the spring resident population occupied units of habitat that were exclusive of other reproductively active individuals. Territorial males were aggregated in blocks of habitat; they formed a central group with territorial females and non-territorial juvenile males occupying peripheral areas. Areas occupied by females were exclusive of other territorial females and the central males, but were overlapped by non-territorial juvenile males in some instances. Throughout the year daily movements of juvenile birds were significantly greater than those of adults with the following exceptions: males in winter and females in summer and autumn. However, in the latter group daily movements of females with broods were greater than those without broods, irrespective of age.

Territoriality among both sexes during the breeding season results in a uniform spacing of members of the population. Such a pattern could have evolved through competition for ecological resources (food and/or breeding space) or as a mechanism to reduce predation. The behavior producing this spacing could also provide a means for adjusting the density of the local breeding population of spruce grouse.

ACKNOWLEDGEMENTS

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J. E. Toepfer, College of Natural Resources, University of Wisconsin - Steven Point, loaned telemetry equipment in 1975 which allowed me to collect the majority of information in this thesis on juvenile male spruce grouse. I also express appreciation for his advice regarding field procedures involving telemetry.

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INTRODUCTION

Studies of tetraonid social behavior have centered on activities of males during the spring season; territorial behavior and courtship displays have been described for males of most species (Hjorth 1970, Wiley 1974). Comparable studies of females do not exist. Female grouse are cryptically colored and lack spectacular displays, thus observation and repeated contact with individuals are difficult as is capture (in some species).

Telemetry provides a means whereby individual grouse can be located at will. This permits one to monitor behavioral parameters in far greater detail than is possible by conventional means (observation of marked individuals) when the study involves secretive animals. Brander (1967), Lance (1970), Robel *et al.* (1970), and Wallestad and Pyrah (1974) used this technique successfully to monitor breeding season movements of female ruffed grouse (*Bonasa umbellus*), blue grouse (*Dendragopus obscurus*) prairie chickens (*Tympanchus cupido*) and sage grouse (*Centrocercus urophasianus*), respectively.

Studies of spruce grouse (*Canachites canadensis*) behavior have emphasized male activity. Stoneberg (1967), McLachlin (1970), Ellison (1971, 1973), and Anderson (1973) describe territoriality, seasonal home range sizes, and habitat selection of males. Lumsden (1961), MacDonald (1968) and Hjorth (1970) describe courtship and territorial behavior. Studies that have emphasized females include those of McCourt (1969) and Haas (1974) who dealt with habitat selection and general aspects of nesting and brood-rearing.

Ellison (1973) suggested that female spruce grouse avoided male territories prior to nesting and nests were located outside male territories.

He also suggested that, because females tended to remain separated from one another during the spring, the possibility existed that they were occupying exclusive areas. MacDonald (1968) recorded aggressive calls of a female spruce grouse while it was attacking a female decoy and suggested such calls given while fighting might space individuals throughout suitable habitat.

Haas (1974) disagreed with Ellison's (1973) suggestion that female spruce grouse might occupy exclusive areas in spring as 16 percent (6 of 37 females), observed during the prenesting period, were with another hen. However, these associations occurred on gravel roads which might have served to attract birds to a common source of grit. Moreover, he stated that females remained apart from one another approximately 2 weeks before the onset of incubation (Haas 1974). There is no information available on daily movements of female spruce grouse nor on the amount of overlap of areas used. Furthermore, a conflict of opinions currently exists (Ellison 1973, Haas 1974) on the spatial relationships between female spruce grouse.

Keppie (1975) documented dispersal of juvenile spruce grouse in fall and spring in southwestern Alberta and speculated that rates of spring dispersal may be correlated with winter population density when the latter rises over a certain threshold. This raises the interesting possibility that spacing of resident adult spruce grouse could be an important factor in the spring movements of juveniles. Therefore, the major objectives of this study were to determine the spacing of adult spruce grouse (with emphasis on females) throughout the year, the extent of behavioral interaction between individuals, and the relationship between dispersion of established residents and the movements of dispersing

juveniles of both sexes. Spruce grouse were chosen for study because they are readily captured permitting the use of radio telemetry on the entire population. The study area chosen supported a population about which background information was available from previous studies (McCourt 1969, McLachlin 1970, and Keppie 1975).

STUDY AREA

This study was done in the eastern foothills of the Rocky Mountains (elevation 1,500 - 2,000 m) near the R. B. Miller Biological Station, 27 km west of Turner Valley, Alberta. The study area encompasses 555 ha adjacent to Gorge Creek (50° 39' N, 114° 39' W).

The forest cover is predominantly a fire-induced growth of lodgepole pine (*Pinus contorta*) with a few small lowland areas dominated by white spruce (*Picea glauca*), isolated clumps of poplar (*Populus* spp.) and scattered small grassy openings. The density of pine varies considerably throughout the forest as does the abundance of alder (*Alnus crispa*) and willow (*Salix* spp.) in the shrub layer. Spruce regeneration also varies throughout the pine forest but greatly exceeds that of pine. Pine trees range from 25 - 38 years in age and 7 - 13 m in height. McCourt (1969) and McLachlin (1970) described the vegetation of the study area in detail and concluded that pine-dominated forest constituted the preferred habitat of spruce grouse but that different sex and age categories used different densities of pine. The study area was divided into sections, the boundaries of which were determined by prominent topographic features. Sections B and C were approximately 0.6 and 1.8 km northwest of section A. Study area boundaries were not rigidly fixed as they were extended when necessary to include the movements of resident birds.

METHODS

I. Field procedures and equipment

A. Locating Grouse

This study extended from April 7 to September 30, 1974, and from January 29 to November 22, 1975. I censused grouse daily on the study area throughout the field season, usually with the aid of pointing dogs. Only with the use of dogs was I able to obtain an adequate coverage of the area for census purposes. I attempted to capture all unmarked birds encountered using a telescopic snare pole (Zwickel and Bendell 1967); these were marked with an individually color-coded sequence of four leg bands. To ensure daily contact with a segment of the population, I attached radio transmitters to all females in given sections of the study area in both years. In the winter of 1975 I radio-tagged several juvenile males; no adult males were radio-tagged in either year. Locating these latter birds depended on the dogs or man.

Radio-tagged grouse were located daily by following the radio signal with a 2 - 4 element hand-held yagi antenna until the bird was observed. When signal reception was erratic and weak because of vegetative and topographic features, I used an 11-element yagi antenna on a 7-meter mast to obtain an initial directional orientation before walking in to the bird with the hand-held antenna. In most cases birds were seen and identified before being overtly disturbed by the observer using this method. Thus, the method was deemed appropriate for recording precise locations. Locations of sightings were recorded from a grid system superimposed on aerial photographs of the study area (1 cm = 50 m).

In 1974, I used telemetry equipment manufactured by Sidney L. Markusen, Electronic Specialties, Esko, Minnesota. Transmitters emitted pulsing signals in the frequency range of 150.815 to 151.150 megacycles. They were originally powered by 12-gram Mallory RM401 mercury batteries with a life expectancy of 90 days. These batteries were replaced soon afterwards by certified 13-gram Mallory RM1 cells with a life expectancy of 180 days when used with the Markusen transmitter. Additional equipment, operating on similar frequencies, was purchased in 1975 from the AVM Instrument Company, Champaign, Illinois. Because the power drain of these transmitters was lower, RM1 batteries had a life expectancy of 500 days. I used Mallory RM640 batteries to lighten the weight of these radio packages when shorter life expectancy (300 days) was adequate.

I attached AVM transmitters as "back-pack" units similar to the method employed by Dumke and Pils (1973). I also modified this method for use with Markusen transmitters; I shortened the battery leads running from the transmitter in order to enclose the battery and transmitter as one complete unit riding on the bird's back. This modification eliminated the need for the battery to ride separately below the bird's crop (Brander 1968), a system of harnessing that requires long battery leads easily severed by a predator with resulting loss of the radio signal. Weights of radio-packages ranged from 13 to 25 g (2 to 5.5 percent of body weight) with most units less than 4 percent of body weight. If birds were harnessed properly, the radio packages appeared not to affect movements, social behavior, or reproductive activities.

B. Studying Behavioral Reactions

To determine behavioral reactions of female grouse to calls of other females, I played these calls to a series of individuals on the study area at intervals throughout the seasons. These calls were first recorded in the field by MacDonald (1968); they were made by a female spruce grouse that was attacking a female decoy. I recorded the reactions of females to these playbacks in the following way: 1) a radio-marked bird was approached until sighted and the presence of any other individuals determined; 2) a portable tape recorder (Sony, Model TC-110) was placed approximately 25 meters from the bird and the playback was switched on; 3) the observer withdrew to a vantage point from which the bird could be observed with binoculars without unduly disturbing it. The first 15 minutes of the tape recording were blank. This allowed time for the bird to adjust to the initial disturbance of discovery. The last 15 minutes of the recording were calls repeated in varying sequence. Changes in the observed bird's behavior were recorded, particularly any vocal responses. After the playback of calls ended, 5 to 10 minutes were allowed to elapse before the observer turned off the recorder and re-checked the surroundings for the presence of other birds. Any birds attracted to the site during the recording were identified at that time.

II. Definitions and methods of analysis

I use dispersion to refer to the spatial distribution of members of a population at one moment in time (Brown and Orians, 1970). To obtain a quantitative measure of dispersion (denoted by the value of R), I used the nearest-neighbor method of Clark and Evans (1954).

Under conditions of minimum dispersion or aggregation (clumped distribution), R=0; in a random distribution R=1; under conditions of maximum dispersion (uniform distribution), R=2.15. To determine which birds in the study area were "nearest-neighbors," I measured the distance between daily locations of all individuals and calculated a mean distance for each seasonal period for all pairs of birds. I also calculated a single seasonal mean distance using all distances between daily locations of nearest neighbors to obtain a measure of dispersion that reflected the actual separation of birds in the field (which I have denoted by the value of D). The area of the largest polygon, enclosing the outermost points of individual locations of all grouse within a given section during any season, was used to determine the total area used in all calculations of R. As pointed out by Brown and Orians (1970), dispersion should not be confused with the term dispersal which refers to the movements of animals (Berndt and Sternberg 1968).

The dispersion of spruce grouse is best presented by seasons that in turn reflect biological events manifested by behavioral changes in the grouse. These seasons include "winter" which began with the formation of flocks and the advent of permanent snow cover and ended when juvenile spruce grouse began moving off known winter ranges. "Early spring" included the period of juvenile wandering; it ended with dispersal of overwintering juveniles. "Late spring" followed, ending with the average date of onset of incubation. Incubation, brood-rearing, and molt were events that occurred during the "summer" season, lasting until the onset of brood break-up. "Autumn" covered the period of brood break-up and dispersal of

juvenile spruce grouse, ending with the advent of permanent snow cover at which time the "winter" population was re-established (Keppie 1975). Grouse were divided into two age-classes, juvenile and adult; grouse were considered as juveniles from their summer of hatching until the following summer when they became first-year adults (July 1).

The size of areas used by individual grouse was determined by computer, using a program designed to calculate the area of a circumscribed polygon. The outer boundaries of the polygon were established by modifying a method described by Harvey and Barbour (1965). This method is based upon the minimum area enclosed by the majority of capture sites. Only those capture sites that were adjacent to another capture site at a distance of less than one-fourth the maximum distance recorded between any two points were included to determine the peripheral locations of the area used. I modified this method by using one-third rather than one-fourth as the critical distance. This permitted the use of at least 95 percent of the locations of sightings of individual birds when establishing the areas used for a particular season. To determine the number of sightings necessary to accurately estimate (95 percent confidence level) the area used by each individual grouse, I used an observation-area curve (Odum and Kuenzler 1955), Appendix 1.

I calculated the distance between successive daily locations of individual grouse to determine minimum daily movements of the grouse. When an individual was located more than once a day, the first location was used to avoid the possibility of bias in movement resulting from the initial contact. When daily movements were analyzed on days with more than one observation, movements between first sightings

on consecutive days (a.m. to a.m.) were significantly higher ($P<0.05$) than within day (a.m. to p.m.) and within night (p.m. to a.m.) movements. Only females with and without broods were exceptions; their rate of travel was similar between consecutive days (a.m. to a.m.) and from p.m. to a.m. (Appendix 2). Early morning and late evening were the periods of greatest travel and both were included in the analysis of daily movements by using the first observation on consecutive days. Student's t-test and analysis of variance (Steel and Torrie 1960) were used to make comparisons between daily movements and between seasonal distances (D).

RESULTS

Dispersion of Female Spruce Grouse

Winter

The areas used by individual adult and juvenile female spruce grouse overlapped extensively during the winter season (Figs. 1 and 2). They were spaced randomly (R=0.97, Table 1) in section A (Fig. 1) but were aggregated (R=0.46, Table 1) in section B (Fig. 2). The mean distance (D) between neighboring females was 179 m in section A and 97 m in section B (Table 2). Two additional females in section A and three in section B died early in the study period. Had they survived, the degree of range overlap of birds during this period would have increased and the R and D values would probably have decreased in both sections. The difference in dispersion values (R) between sections A and B may have been caused by larger expanses of suitable winter habitat in section A allowing birds to spread out over larger areas. Female 2 (14 sightings, Fig. 1) and female 15 (11 sightings, Fig. 2) were not radio-tagged during the winter period and females 3 and 4 (10 and 11 sightings, respectively, Fig. 1) were not captured and radio-tagged until late March when the study area boundary was extended; the number of sightings of these females was insufficient to accurately estimate their winter areas as their observation-area curves were still rising (Odum and Kuenzler 1955) with each additional location (Appendix 1). These birds appeared to occupy areas similar in size to those of other individuals in the winter population and their locations were considered in determining R and D values.

The size of areas used by 10 juvenile females, including females 43 and 69 located in section C of the study area, ranged from 0.6 to

Figure 1. Spatial relationships among 10 female spruce grouse during the winter season in section A (February 8 - April 11, 1975). Females 1-4 are adults.

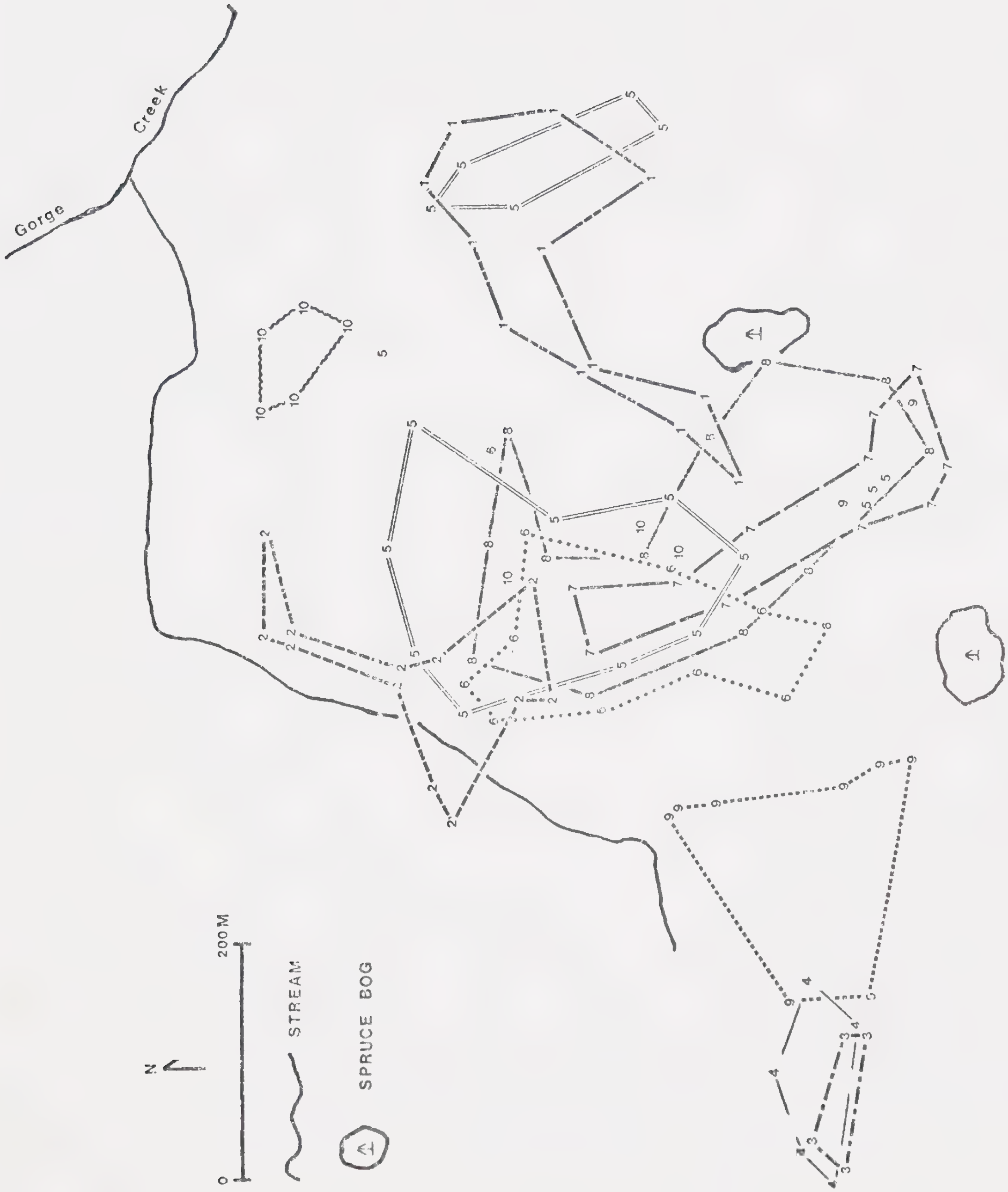
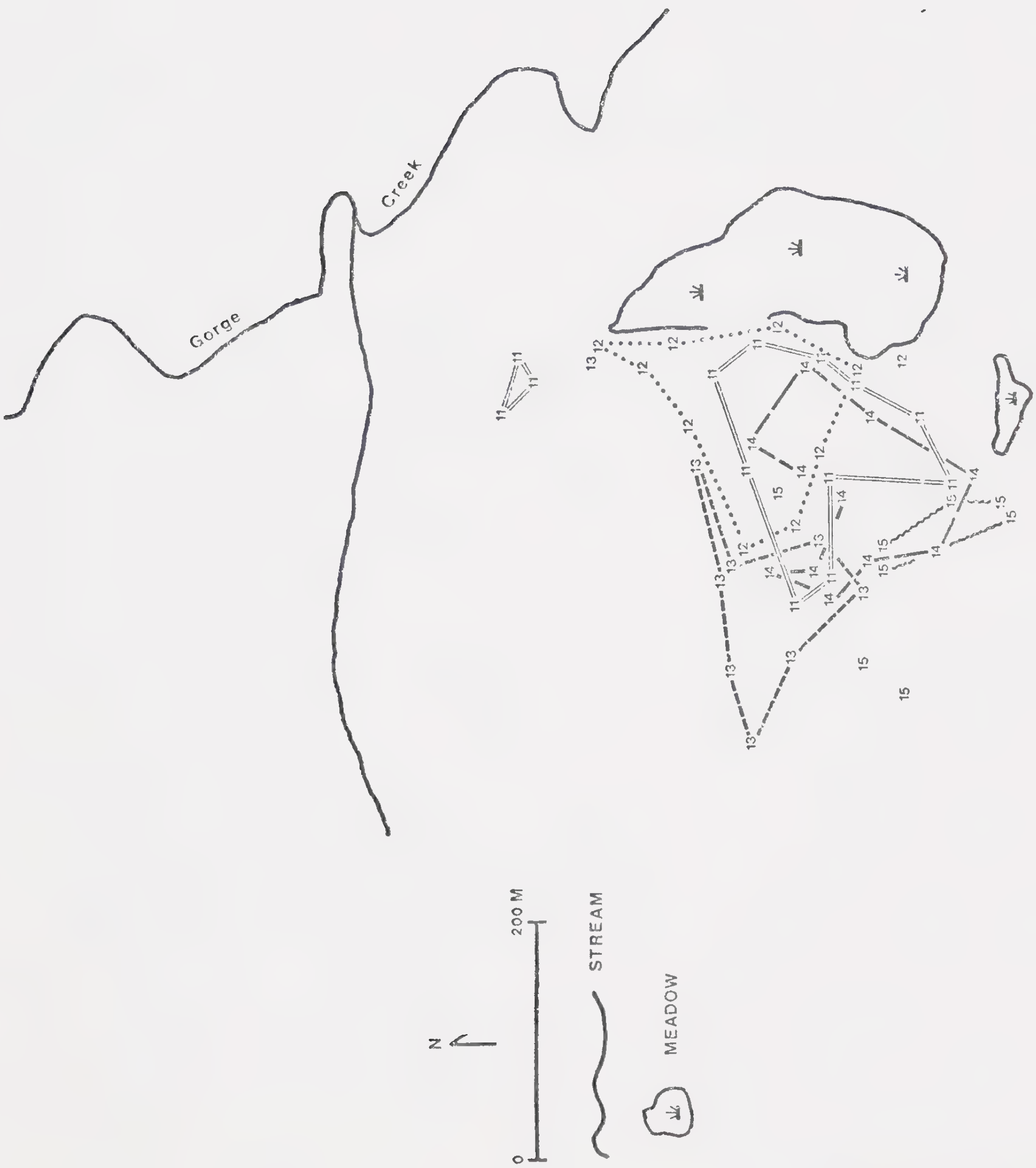

Gorge Creek
N
0
200 M
STREAM
SPRUCE BOG

Figure 2. Spatial relationships among five female spruce grouse during the winter season in section B (February 3 - April 11, 1975). Females 11, 13 and 15 are adults.



Gorge Creek
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MEADOW

Table 1. Dispersion values (R) for the spatial relationships between nearest neighbor female spruce grouse during all seasons in 1974 and 1975.

Study area section	Year	Winter	E. Spring	L. Spring	Summer	Autumn
A	1975 Ad.	-	-	-	-	0.93[1]
	All	0.97[1]	0.99[1]	1.86[3]	1.51[3]	1.28[1]
B	1974 Ad.	-	1.90[3]	-	-	-
	All	-	1.40[3]	2.09[3]	1.63[3]	-
B	1975 All	0.46[2]	0.78[1]	1.89[3]	-	-
C	1975 All	-	-	1.96[3]	-	-

[1] random

[2] significantly aggregated ($P<0.05$)

[3] significantly uniform ($P<0.05$)

Table 2. Mean ($\bar{x}$) distance (D) in meters, plus and minus one standard deviation, between nearest-neighbor female spruce grouse during each season in 1974 and 1975.

Study area section	Year	Winter			E. Spring			L. Spring			Summer			Autumn		
		$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
A	1975 All	179	136	333	189	205	239	363	190	110	328	260	232	252	207	322
B	1974 Ad.		-		303	145	92									
	All		-		177	120	131	315	144	78	302	189	225		-	
B	1975	97	110	222	175	145	102	360	176	52		-			-	
C	1975		-			-		335	158	52		-			-	

7.0 ha during the winter season (Table 3). Five adult females, including females 41 and 42 located in section C, occupied significantly smaller areas ($P<0.05$), ranging from 0.08 to 3.0 ha (Table 3). Those females presented in Figs. 1 and 2 (i.e., female 2, Fig. 1), that were not located a sufficient number of times to accurately estimate area size, are not listed in Table 3.

Daily movements of adult females in winter ($\bar{x}$ = 37 m) were significantly lower ($P<0.05$) than daily movements of juvenile females ($\bar{x}$ = 53 m, Table 4). Both radio-tagged and banded females of both ages often spent several days in small areas (0.1 to 0.25 ha) and occasionally were located in the same tree on 3 or 4 consecutive days; in these instances daily movement was recorded as zero. Indirect evidence, based on the amount of droppings beneath these trees during periods of snowfall, indicated that movements away and back from these trees occurred on the same day on some occasions. Most individuals returned to the same tree or clump of trees on several occasions after variable periods of absence. These "favorite" trees were used by different individuals and may represent preferred areas of habitat used for feeding and roosting. Winter flocks occasionally aggregated at these sites, possibly because of characteristics of these trees or the surrounding habitat.

Early Spring

Daily movements by both juvenile and adult females increased significantly ($P<0.01$) above winter levels during the early spring season (Table 4). At this time as during winter, the movement of juveniles (179±215 m) was significantly farther ($P<0.01$) than adults

Table 3. Size of areas in hectares occupied by adult and juvenile female spruce grouse during each season of 1974 and 1975.

			Season				
Female no.	Age	Year	Winter	E. Spring	L. Spring	Summer	Autumn
			Area N	Area N	Area N	Area N	Area N
5	Juv.	1975	7.0(40)	18.9(33)	5.8(26)	15.2(53)[1]	12.4(38)
6			3.5(54)	37.9(33)	4.9(25)	27.7(59)[1]	22.7(54)
7			2.6(52)	7.7(25)			
8			7.0(56)	15.0(29)			
9			3.3(21)	16.9(32)			
10			0.6(52)	10.0(32)			
12			2.3(68)	5.3(37)	1.7(25)		
14			2.2(71)	9.3(38)	8.6(18)		
43			3.2(35)	14.4(29)	14.9(22)		
69			3.9(33)	18.3(30)			
		$\bar{x}$±SD	3.6±2.0	15.4±9.1	7.2±5.0		
1	Ad.	1975	3.0(38)	4.8(32)	3.4(18)		
2					4.4(23)	7.4(47)[1]	5.9(44)
3				3.1(26)	0.6(21)		
11			2.5(67)	7.4(40)	1.2(20)		
13			1.3(70)				
41			0.8(37)	4.0(29)	1.3(14)		
42			2.8(34)	3.4(30)	2.3(15)		
		$\bar{x}$±SD	2.0±1.0	4.5±1.7	2.3±1.4		

continued...

Table 3. continued

Female no.	Age	Year	Winter	E. Spring	L. Spring	Summer	Autumn
34	Ad.	1975				8.2(44)[1]	16.0(52)
46						37.7(34)[1]	12.7(30)
47						8.0(25)[1]	5.0(43)
		$\bar{x}$±SD				15.9±7.2	11.1±6.0
11	Juv.	1974			9.3(37)	11.2(63)[1]	
18	Ad.			2.3(18)			
19				3.0(35)	1.3(35)		
20				5.5(37)	2.2(38)	20.6(44)[2]	
21				6.5(53)			
22				0.8(26)	2.0(22)		
23					3.9(30)	20.3(63)[2]	
71						21.5(39)[2]	
72						17.3(57)[1]	
73						26.4(74)[2]	
74						35.3(41)[2]	
75						50.1(41)[2]	
76						9.4(43)[1]	
77						16.7(52)[1]	
	$\bar{x}$±SD			3.6±2.3	2.3±1.2	15.0± 9.7[1] 29.0±11.8[2]	

[1] Females without broods

[2] Females with broods

Table 4. Mean ($\bar{x}$) seasonal daily movements in meters of adult and juvenile female spruce grouse in 1974 and 1975.

		Season														
Age	Year	Winter			E. Spring			L. Spring			Summer			Autumn		
		$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Ad.	1974		-		104	96	108	128	99	79	134	107	214[1]		-	
											200	127	220[2]			
Ad.	1975	37	46	252	101	104	185	151	122	88	139	110	220[1]	162	135	245
Juv.	1975	53	66	442	179	215	317	234	179	102		-[3]		181	160	40

[1] Females without broods

[2] Females with broods

[3] No juvenile females monitored this season

(101±104 m). Areas used by individual female grouse continued to overlap greatly during early spring (Figs. 3 and 4) but the size of the individual areas used increased dramatically for juvenile and to a lesser extent for adult females (Table 3). Juvenile female 6 in section A (Fig. 3) occupied the largest area recorded (37.9 ha).

In section A (Fig. 3), the mean distance between nearest neighbors (D) remained similar (P>0.05) to the winter season (Table 2) and dispersion remained random (R = 0.99, Table 1). In section B (Fig. 4) the mean distance between nearest neighbors increased to 175 m (Table 2) and dispersion was not significantly different (P>0.05) from randomness (R=0.78, Table 1).

Juvenile females often moved long distances away from the area normally used, returning to it the following day. These excursions may have given them the opportunity to investigate new habitat. Over-wintering juvenile females 7, 8, 9 and 10 left section A permanently (Fig. 3) during spring dispersal of 1975. Emigration of these juveniles coincided with the appearance of the first new juveniles on the study areas (females 33, 34 and 35, Fig. 3, and 16, Fig. 4). Daily movements of juvenile females emigrating during spring dispersal are presented in Appendix 3.

The movements of most resident adult females remained centered on the winter range (Figs. 1, 2, 3 and 4). The areas used by some adults shifted short distances during this period, for example female 11 (Figs. 2 and 4). Migratory adult females (Keppie 1975), wintering on the study area, left during this period (females 4, Fig. 3, and 13 and 15, Fig. 4) and migratory adult females (female 23, Fig. 5) returned to breed. Thus,

Figure 3. Spatial relationships among 13 female spruce grouse during the early spring season in section A (April 12 - May 15, 1975). Females 1-4 are adults.

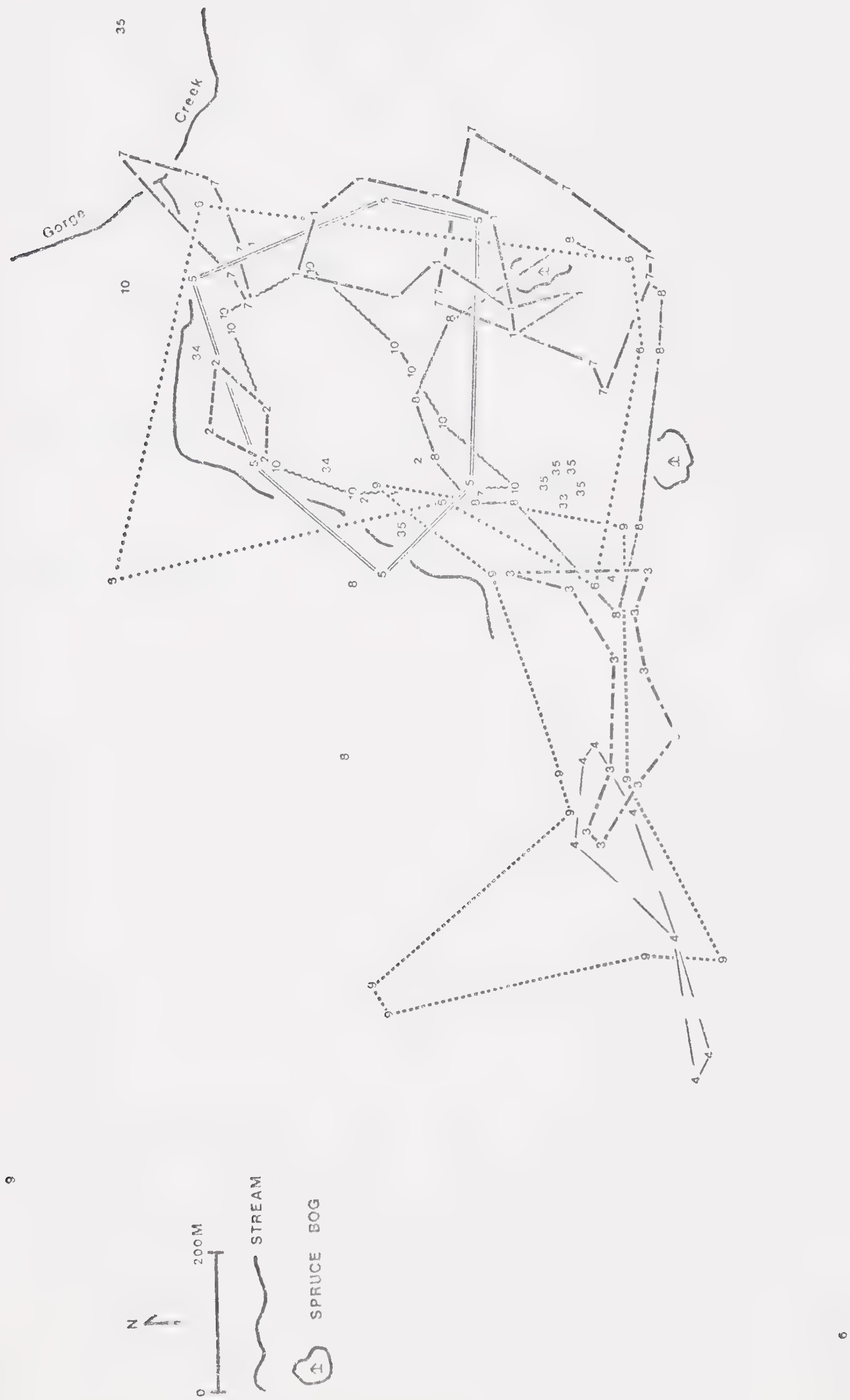
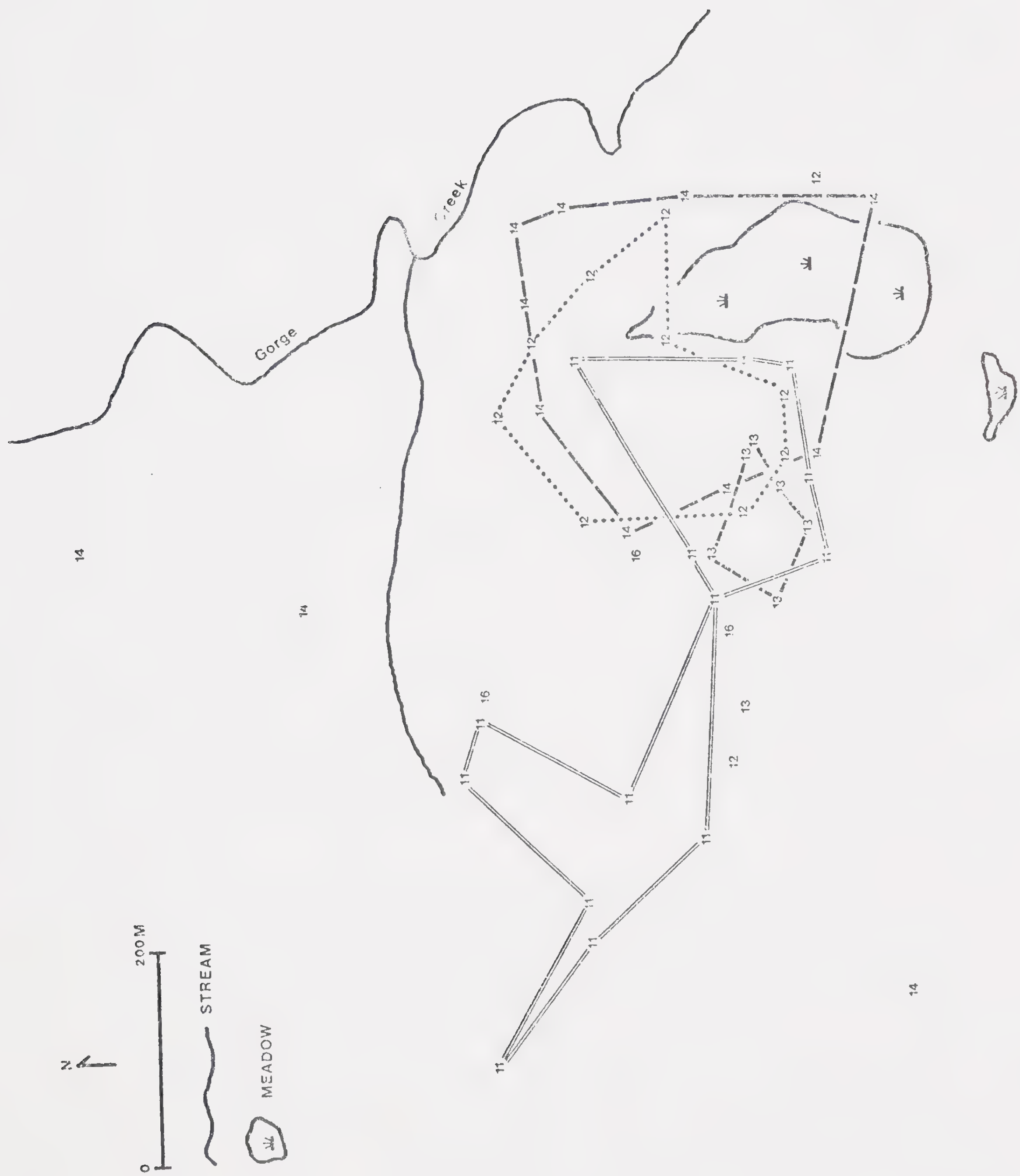

Gorge
Creek
N
0
200M
STREAM
SPRUCE BOG

Figure 4. Spatial relationships among six female spruce grouse during the early spring season in section B, 1975 (April 12 - May 22). Females 11 and 13 are adults.


Gorge Creek
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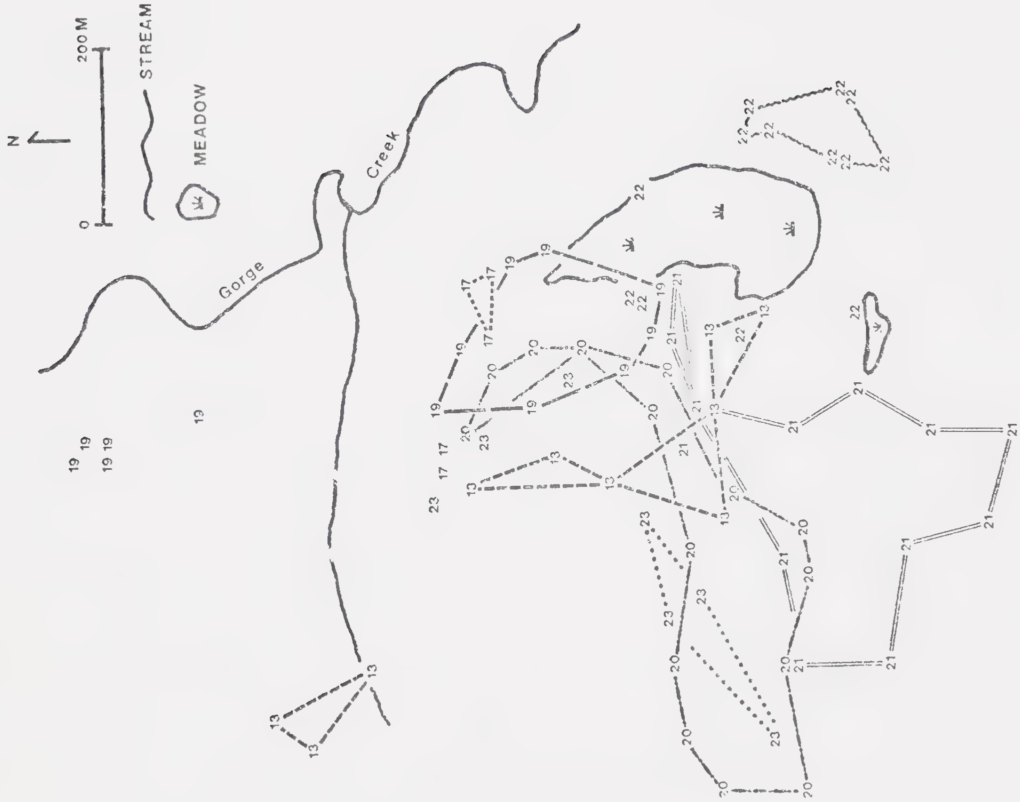
MEADOW

the individuals involved and the resulting density and dispersion of females changed. Daily movements of adult females during spring migration are presented in Appendix 3.

The distribution of adult and juvenile females on section B in 1974 is depicted in Figs. 5 and 6. In that year, the density was higher than in 1975 (13 vs. 5) and the dispersion of adult females (Fig. 5) was uniform (R = 1.9, Table 1) with a mean distance between nearest neighbors of 303 m (Table 2). The areas used by females 19 and 20 shifted over this period of early spring observations. Female 19 settled in the isolated north section of its area and female 20 in the northeast section of its area (Fig. 5). This movement of female 20 into the vacated area of female 19 accounts for the apparent overlap area of these two individuals shown in Fig. 5. Female 23, a migrant breeding on section B, did not establish a breeding range until female 20 had vacated the southwest segment of its area. Female 17 was not radio-tagged during this period and consequently its area is not well known. Daily movements (Table 4) and size of areas used (Table 3) by adult females in 1974 were similar to those for adult females in 1975 (Tables 3 and 4).

Seven juvenile females overwintered in section B in 1974. In early spring, their areas of use overlapped each other (Fig. 6) and those of adult females (Fig. 5), a situation also seen in 1975 (Figs. 3 and 4). Only two juvenile females were successfully radio-tagged (females 27 and 28); both left the study area during spring dispersal, as did females 24 and 26. Two juvenile females died because of improper harnessing with the radio package (females 29 and 30) and a third (female 25) was lost to a predator. Since too few locations were obtained on banded individuals and transmitters were removed from radio-tagged

Figure 5. Spatial relationships among seven adult female spruce grouse during the early spring season in section B, 1974 (April 9 - May 25).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200 M
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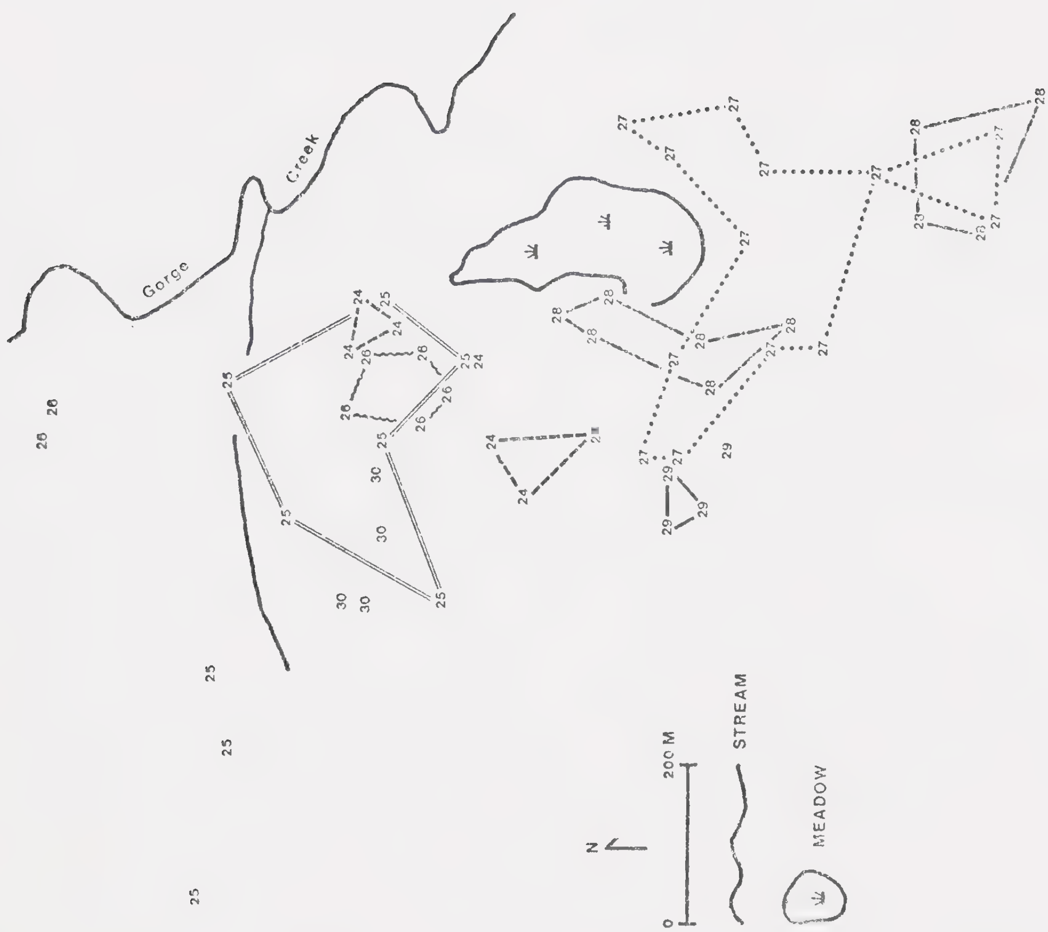
Figure 6. Spatial relationships among seven juvenile female spruce grouse during the early spring season in section B, 1974 (April 9 - May 25).



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juveniles as soon as they left the section for the first time, I could not accurately determine either daily movements or sizes of areas used. The mean distance between nearest neighbors dropped to 177 m from 303 m (Table 2) with the inclusion of all seven juvenile females. The nearest-neighbor dispersion value (R) also decreased from 1.9 to 1.4 indicating a less uniform distribution of individuals (Table 1).

Late Spring

All female spruce grouse were uniformly spaced (R = 1.86 - 2.09, Table 1) and occupied essentially exclusive areas that were separate from males during spring (Figs. 7, 8, 9 and 10). Mean daily distances between nearest neighbors (D = 315 - 363, Table 2) were significantly higher ($P<0.01$) than in previous seasons. Three juvenile females (31, 32 and 34) immigrated to section A of the study area (Fig. 7) and established breeding areas in habitat largely unoccupied by resident females. Female 35 spent 6 days in section A before travelling to section B (Fig. 8). Only one overwintering juvenile female (6) remained in section A during the breeding season. Female 5 overwintered in section A and is included in Fig. 7 - its area extended past the original boundary of the study area.

Although the area occupied by female 35 in Fig. 8 appeared to completely overlap that of female 36, several locations of female 35 responsible for this overlap were recorded before the arrival of female 36. Female 12 established its breeding range in the same area as its winter range (Fig. 2) while female 14 moved to the northwest. Female 38 was captured late in the season when the study area boundary was extended (Fig. 8). Female 16 was killed 4 days after radio-tagging (Figs. 4 and

Figure 7. Spatial relationships among nine female spruce grouse during the late spring season in section A (May 16 - June 9, 1975); stippled areas occupied by territorial male spruce grouse. Females 1-3 are adults.

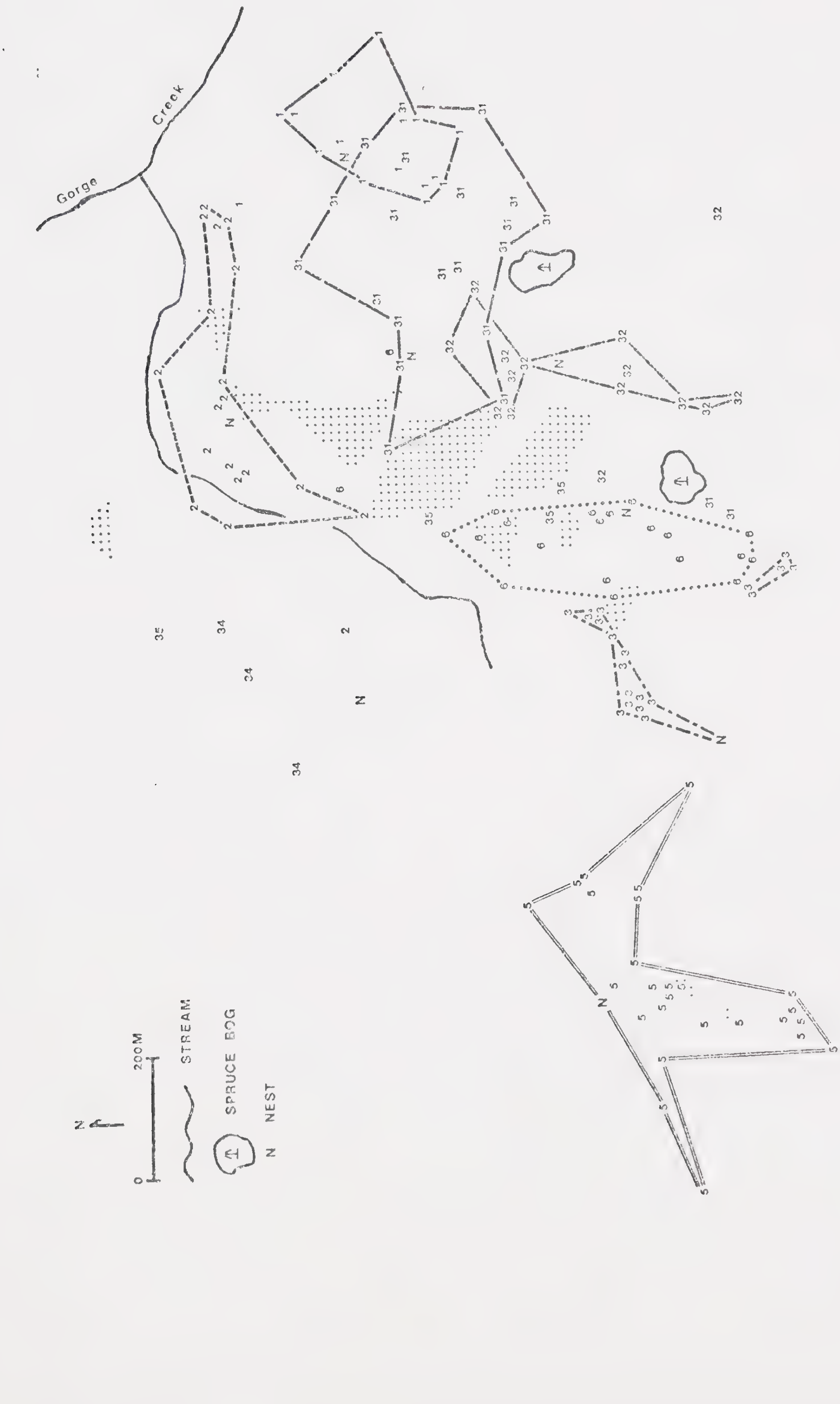
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Figure 8. Spatial relationships among seven female spruce grouse during the late spring season in section B, 1975 (May 23 - June 11); stippled areas occupied by territorial male spruce grouse. Female 11 is an adult.

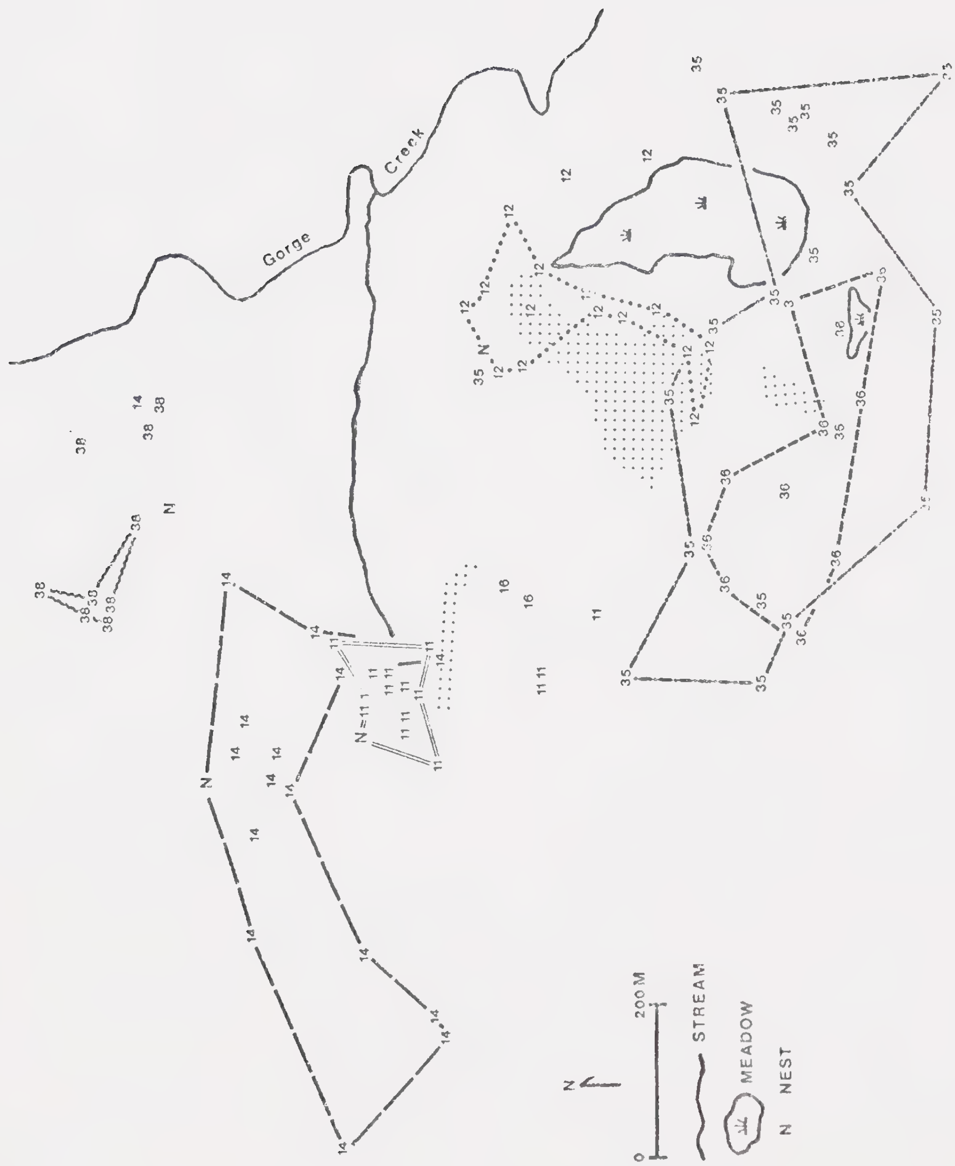
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Figure 9. Spatial relationships among eight female spruce grouse during the late spring season in section B, 1974 (May 26 - June 19); stippled areas occupied by territorial male spruce grouse. Females 17, 19, 20, 21, 22 and 23 are adults.

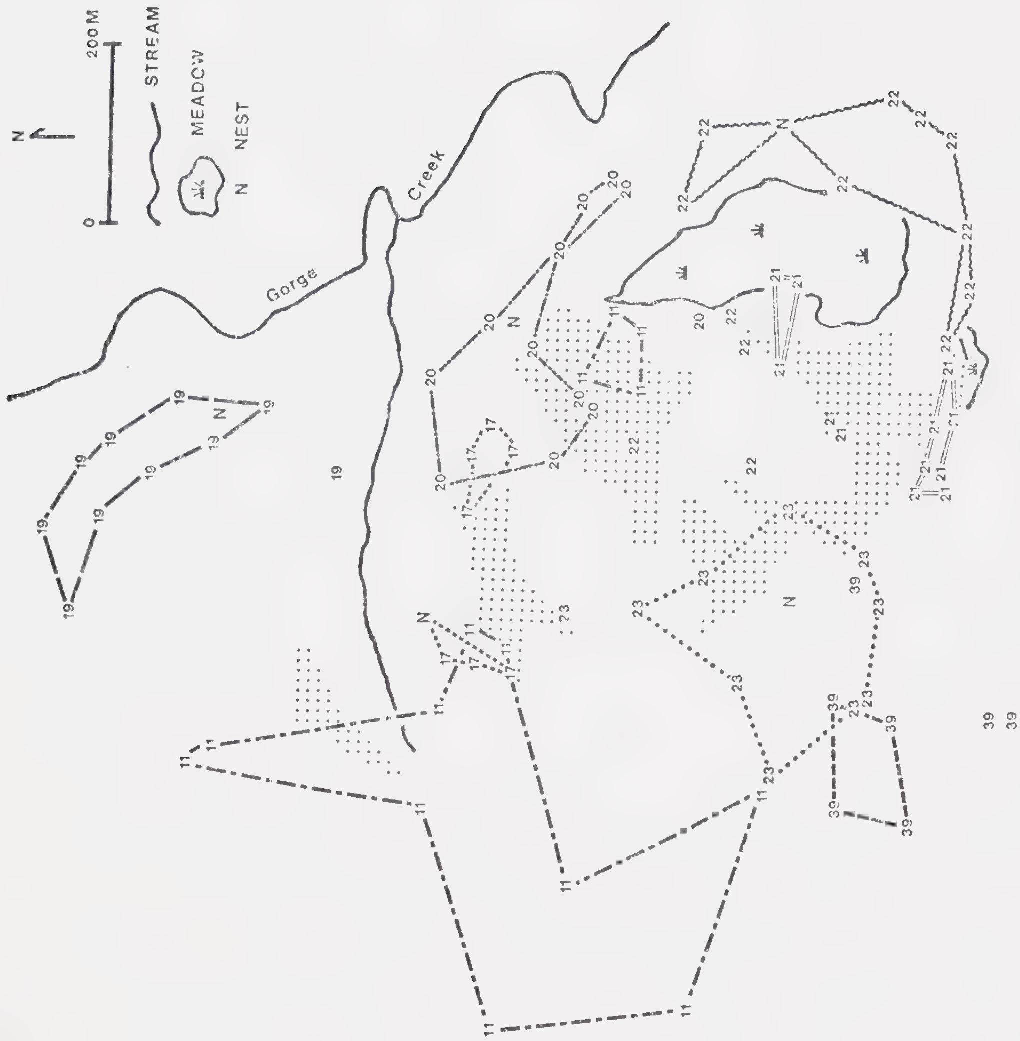
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Figure 10. Spatial relationships among five female spruce grouse during the late spring season in section C (May 14 - June 12, 1975); stippled area occupied by territorial male spruce grouse. Females 41, 42 and 45 are adults.


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8). Female 11 (Fig. 8) remained in the area to which it had moved from winter range (Fig. 2) and this area coincided with a part of its range in 1974 (Fig. 9).

Fig. 9 shows the distribution of female spruce grouse on section B during the 1974 late spring period. Females 11 and 39, juvenile immigrants, established themselves in unoccupied habitat. Resident adult females remained in the same general areas that they occupied at the end of the early spring period (Figs. 5 and 9). Five additional female spruce grouse were radio-tagged in 1975 on a separate part of the study area and their pattern of distribution was similar to that of the other areas monitored (Fig. 10), namely uniform ($R = 1.96$, Table 1).

The size of areas occupied by adult females in late spring averaged 2.3 ha in both years (Table 3). This size was significantly smaller ($P<0.05$) than that occupied in late spring (7.2 ha) by overwintering juvenile females which remained in the study area in 1975 (Table 3). Immigrant juvenile females were recorded occupying the largest areas (12.2 ha ± 4.1, $n = 3$) probably because locations used in measuring this area included those recorded upon their arrival on the study area, a time when these birds apparently were still searching for an appropriate space. Both age-classes of females occupied areas in late spring which were smaller than those occupied in early spring (Table 3).

Daily movements increased significantly ($P<0.01$) for both age-classes of females during the late spring season in 1975 (Table 4); adult females moved a significantly lesser mean daily distance (151 m) than juvenile females (234 m) (Table 4). Adult females moved at a lesser rate in 1974 than in 1975 (Table 4); the two juvenile females radio-tagged

in 1974 moved a minimum daily distance of 162 m which was also less than the rate for juvenile females in 1975.

Nests were located for all adult and some juvenile females; nest sites are included in Figs. 7 - 10. Nests were often positioned at the edge of a female's area, possibly outside areas of heavy use. Nest sites were uniformly spaced as a result of the separation of female areas in late spring (R = 1.7, 1.9, 2.0 and 1.6, Figs. 7 - 10, respectively).

Nests were not found for juvenile females 35, 36 and 45 in 1975 and 39 and 40 in 1974. Female 39 was recaptured in early July to replace a faulty transmitter and had a well-developed brood patch at this time - radio transmission failed in early June before any evidence of nesting was obtained. Although no evidence of nesting activity was obtained for the other four juvenile immigrant females, movements were localized and nests may have been destroyed before discovery.

Areas used by both juvenile and adult females were separate from those used by displaying males and were established on the periphery of the main aggregations of these males (Figs. 7 - 10). Females therefore did not nest on male territories. Juvenile males that did not establish defined territories moved within the areas occupied by female grouse. These juvenile males did not display or respond to tape recordings of female calls; displaying males always responded immediately with courtship behavior.

A degree of overlap in space between male and female grouse must exist for copulation to occur; females were located on occasion in the presence of males near the peripheries of male territories. Territorial males were also observed far from their territories on some occasions (e.g. male 5, Fig. 19) possibly in pursuit of females or in the avoidance of predators.

Summer

Female spruce grouse ceased to occupy exclusive areas immediately after either nest destruction or hatching and areas of use again overlapped considerably (Figs. 11 and 12). The pattern of dispersion was significantly different ($P<0.05$) from random as R values were 1.51 in section A (Fig. 11) and 1.63 in section B (Fig. 12) (Table 1). Mean daily distances between nearest neighbors remained similar to the previous period in both section A (328 m) and section B (302 m) (Table 2). Thus, areas of use overlapped but females were seldom observed in close proximity to one another, separation being maintained temporally rather than spatially. No females nested successfully in section A (Fig. 11); females 1, 3 and 31 (Fig. 7) died shortly after their nests were destroyed and are not shown in Fig. 11.

New females were added to the groups on both sections of the study area during summer (46 and 47, Fig. 11 and 48, 49 and 50, Fig. 12). This happened because the area censused had increased through the expansion of areas used by radio-tagged birds and females moved from late spring areas (i.e. female 19, Figs. 8 and 12) to new areas. The three new females in Fig. 12 had been banded previously in an area adjacent to section B and were radio-tagged early in summer. Their subsequent movements in turn expanded the study area boundary but no attempt was made to search this new area for other female grouse.

Females moved over larger areas in summer than during any other season; females with broods occupied the largest areas averaging 29.0 ha (Table 3). Female 46 (Fig. 11) wandered over an area of 37.7 ha during the summer - the largest area occupied by any other female without a brood was 27.7 ha (female 6, Fig. 11). Females with broods

Figure 11. Spatial relationships among seven adult female spruce grouse during the summer season in section A (June 12 - September 1, 1975).

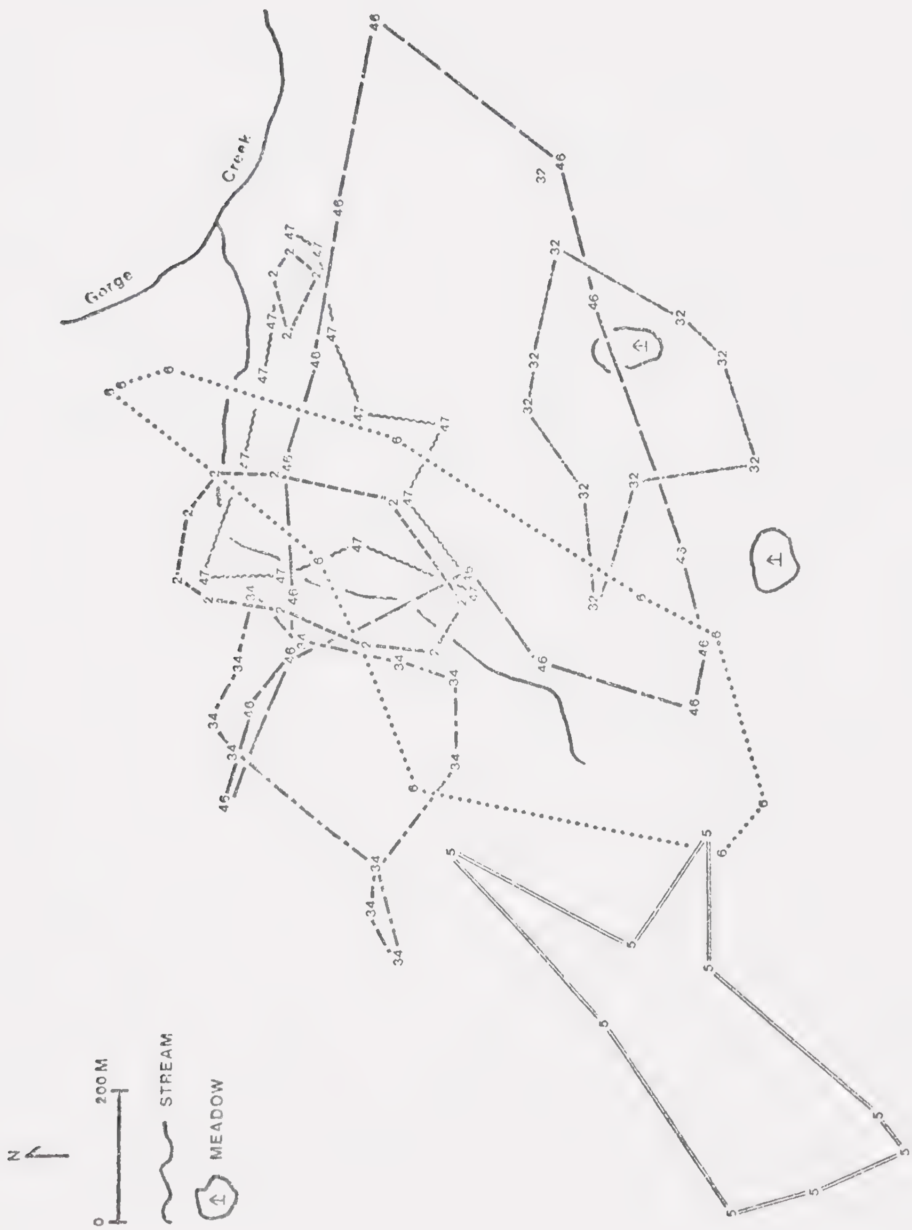
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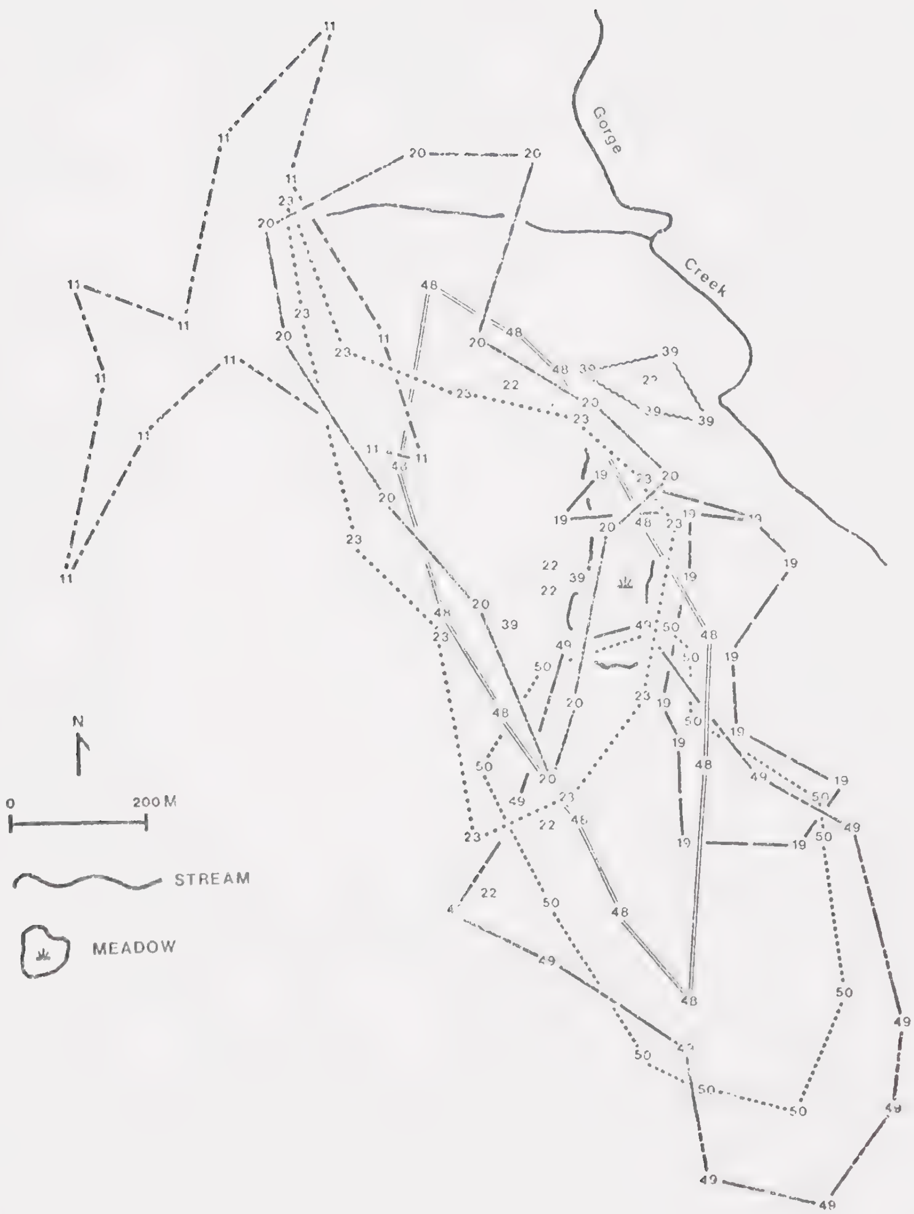
Figure 12. Spatial relationships among nine adult female spruce grouse during the summer season in section B (June 22 - September 1, 1974).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and those without occupied the same general areas of the study area (Fig. 12) although females with broods often selected forest openings, confirming McCourt's (1969) observations.

During the summer season in both years, females without broods moved significantly less ($P<0.01$) than females with broods (Table 4). Females with broods moved at the highest rate (200 m) of adult females at any season (Table 4) which may reflect travel necessary to acquire adequate food for growing chicks (juveniles).

Autumn

Section A in 1975 was the only area monitored during the autumn period. Early in the season before the first juvenile immigrants arrived, adult females were randomly dispersed ($R = 0.93$, Table 1) and the mean distance between nearest neighbors (D) was 221 m (Table 2). Adult females occupied the same general areas as during the summer season and overlap between individuals remained extensive (Figs. 11 and 13). Migratory female 7 arrived in mid-September, migratory female 46 departed in early October, and the switch in the area used by female 5 (Figs. 11 and 13) altered the composition of adult females in the study area.

Juvenile females entered the area in early October when four individuals were captured and radio-tagged. Unlike the late spring period, no attempt was made to select areas of unoccupied habitat (Fig. 14); they were often found together with adult females. However, the dispersion value (R) increased significantly toward uniformity ($R=1.28$) with the inclusion of these juveniles in the autumn population (Table 1). The mean distance between nearest neighbors of 227 m after the immigration

Figure 13. Spatial relationships among eight adult female spruce grouse during the autumn season in section A (September 2 - November 17, 1975).

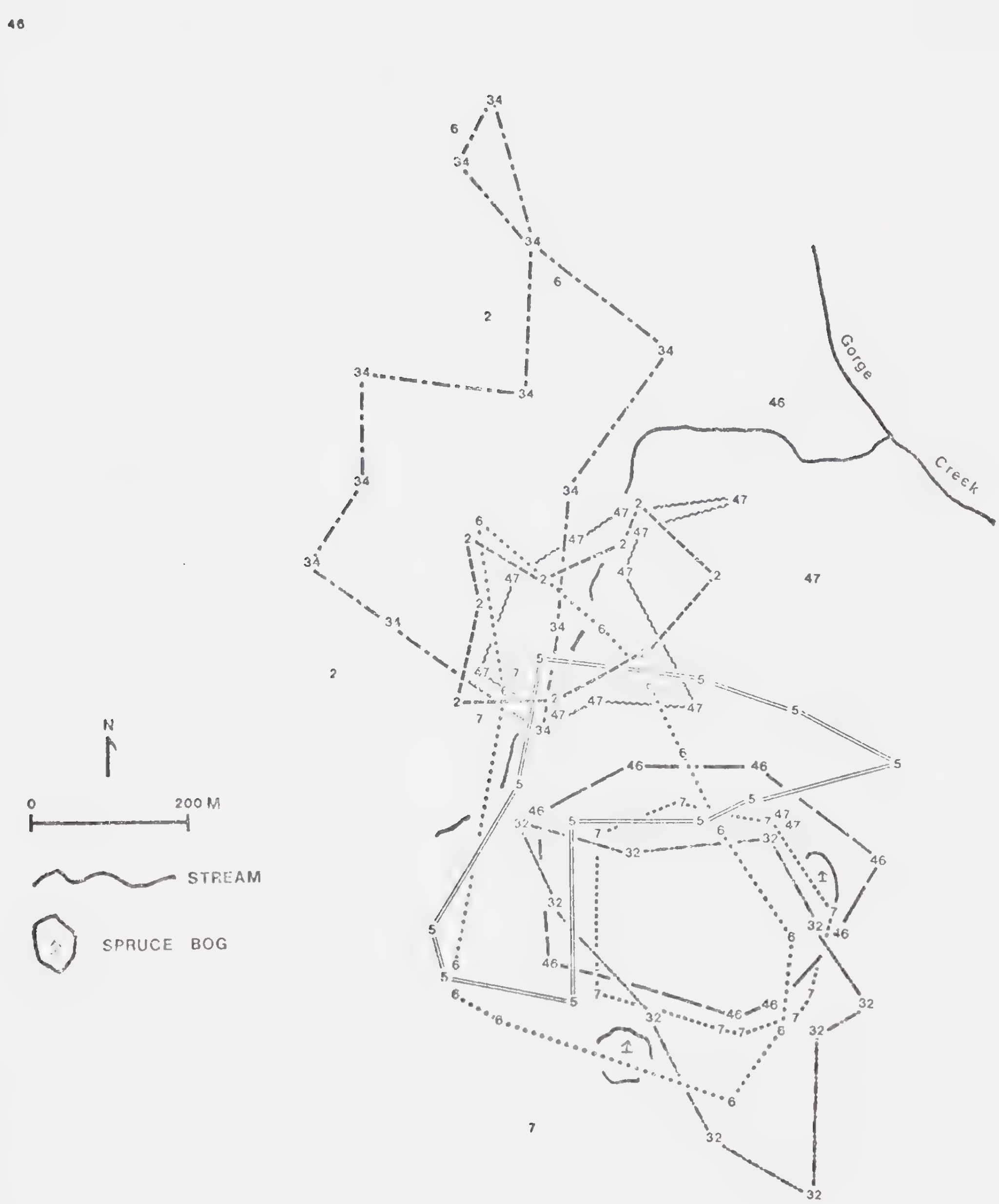

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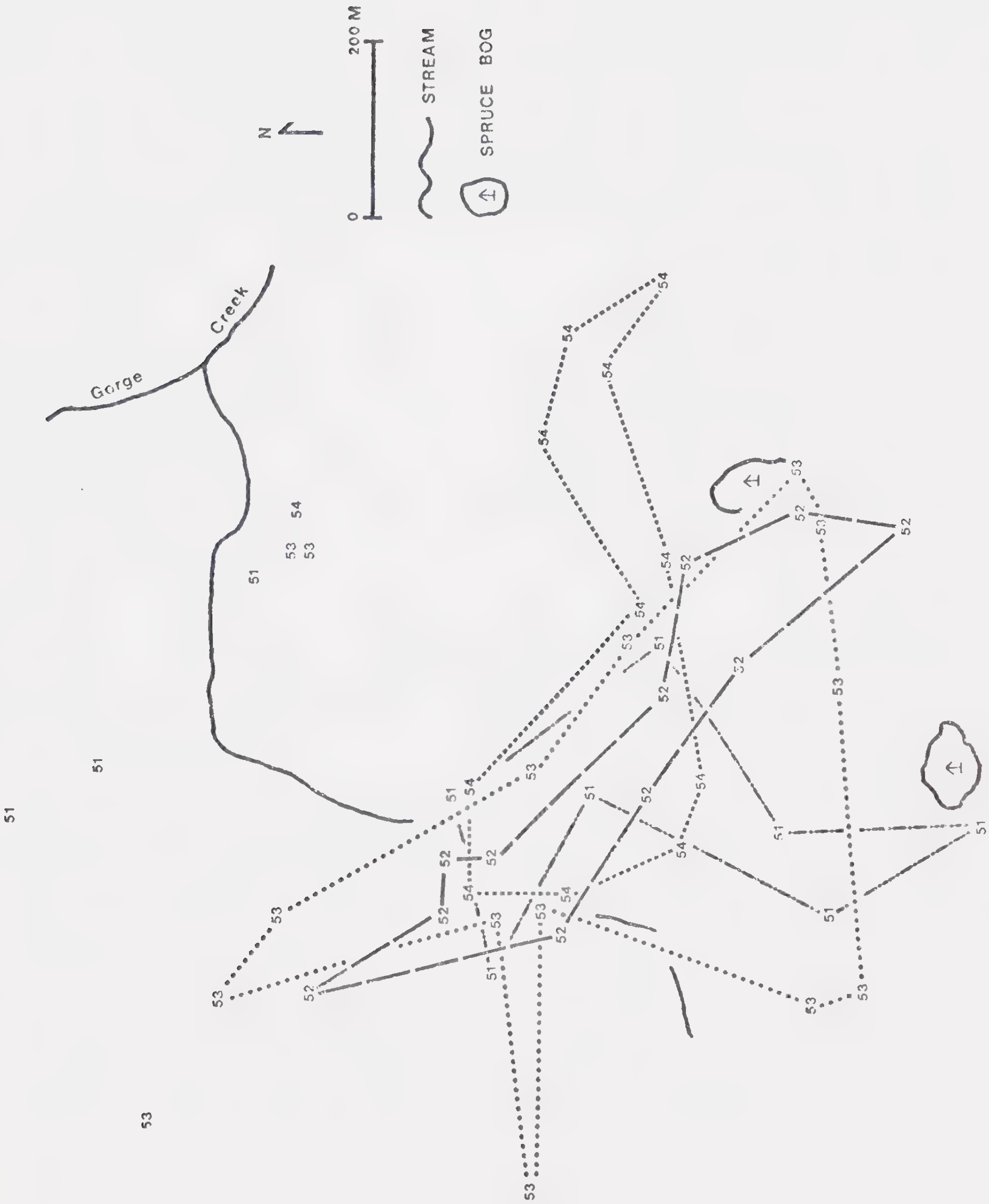
Figure 14. Spatial relationships among four immigrant juvenile female spruce grouse during the autumn season in section A (October 10 - November 17, 1975).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of juvenile females was similar to a mean distance of 221 m between adult females before their arrival (Table 4). Thus, it appeared that juvenile females were spacing themselves in relation to other females on the study area. Female 54 left the area on November 14 and was recaptured three days later 3 km away - females 51 and 52 remained on the area for the winter. The fate of female 53 was unknown as radio contact was lost on October 24 and she was not resighted on the study area.

Adult females occupied areas in autumn similar in size to those of broodless females in summer ($\bar{x}$ = 12.5 ha, Table 3). By late October with the first days of snow cover, females restricted their movements to smaller areas. However, the study was terminated before this aspect could be documented quantitatively. Juvenile females 51, 52 and 53 occupied areas estimated at 4.6, 5.8 and 6.3 ha, respectively but insufficient observations were made to accurately estimate the size of areas used as area sizes were still increasing. Juvenile female 54 ranged over 16.7 ha before it left the study area.

Daily movements of adult females averaged 162 m in autumn, a rate similar to late spring movement (Table 4) in 1975, with an occasional long distance excursion. Immigrant females moved an average of 181 m daily (Table 4). This mean rate of daily movement did not differ significantly ($P>0.05$) from that of adult females, unlike the late spring season when juvenile females moved at a much higher rate (Table 4).

Dispersion of Male Spruce Grouse

Winter

Adult male spruce grouse were seldom found together, apparently avoiding areas occupied by other adult males during the winter (Figs. 15 and 16). The pattern of distribution was random for adult males in Fig. 15 (R = 1.19, Table 5). This measure of dispersion, based on few sightings, may not be accurate as some individuals were located at long distances from the locations of major use (males 4, 5 and 6, Fig. 15). Males 1 and 2 (Fig. 15) died early in the winter in section A thus providing few observations.

By contrast, juvenile male spruce grouse were often found together and their areas of use overlapped each other considerably (Figs. 15 and 16). Overlap between areas used by juvenile and adult males was variable; areas used by the two age-classes appeared essentially exclusive in section A (Fig. 15) whereas considerable overlap between areas existed in section B (Fig. 16). The dispersion of all males in winter was random (R = 0.70, Fig. 15, and R = 0.76, Fig. 16, Table 1). I radio-tagged five juvenile males during the last 2 weeks of winter which accounted for the higher number of sightings of them (males 10, 11 and 12, Fig. 15; 12 and 15, Fig. 16). Male 12 moved between sections A and B during this period (Figs. 15 and 16).

The size of areas occupied by juvenile male spruce grouse ranged from 1.9 - 14.7 ha (Table 6). Only one adult male (17, Fig. 16) was observed a sufficient number of times to determine the size of the area occupied - 2.1 ha. Extrapolating from the observation-area curve (Appendix 1), it appeared that most adult males occupy areas of 1.5 - 2.5 ha in winter. Mean daily movements of adults and juveniles were

Figure 15. Spatial relationships among 13 male spruce grouse during the winter season in section A (February 8 - April 11, 1975). Males 1-8 are adults.

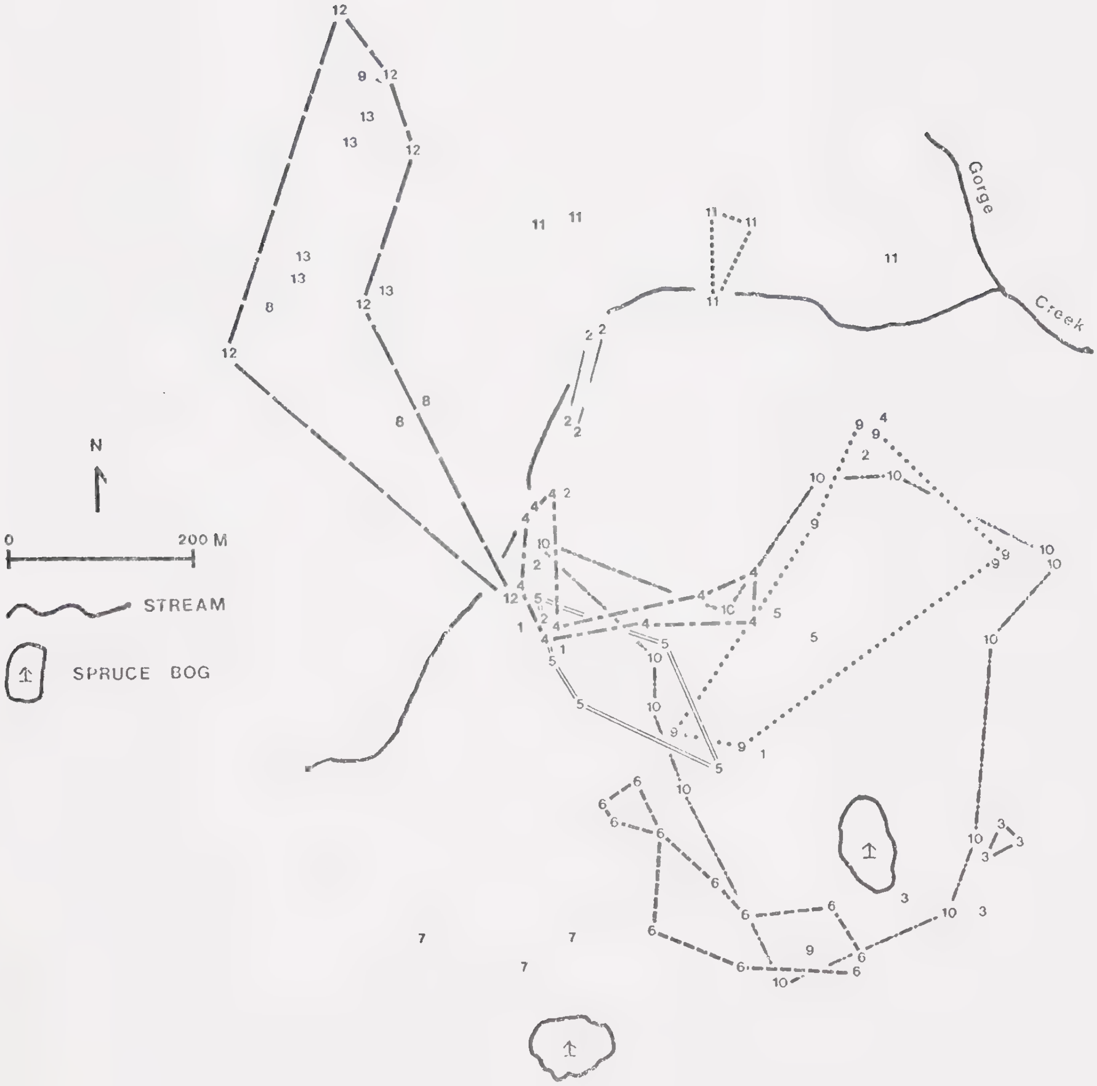
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Figure 16. Spatial relationships among eight male spruce grouse during the winter season in section B (February 3 - April 11, 1975). Males 16-19 are adults.

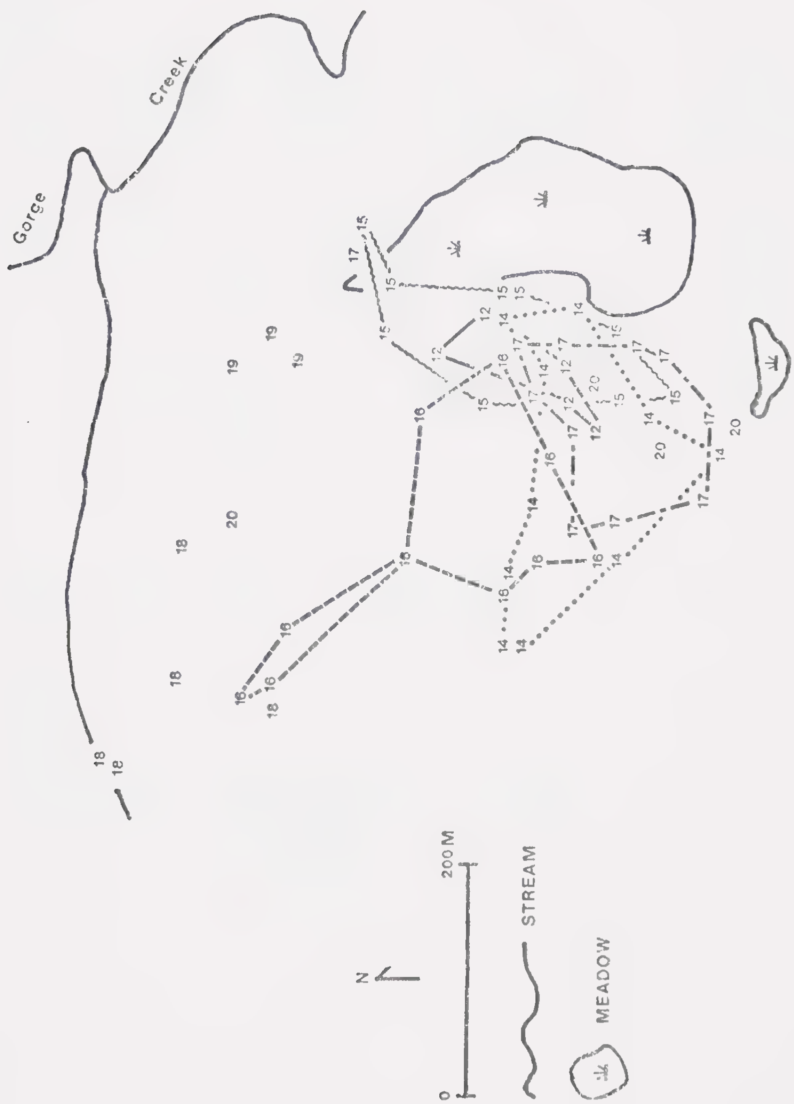
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Table 5. Dispersion values (R) for the spatial relationships between nearest-neighbor male spruce grouse in 1974 and 1975.

		Season		
Study area section	Year	Winter	E. Spring	L. Spring
A	1975 Ad.	1.19[1]	-	1.93[3]
	All	0.76[1]	0.84[1]	0.96[1]
B	1974 Ad. (All)	-	-	1.60[3]
B	1975 All	0.70[1]	-	-

[1] random

[2] significantly aggregated ($P < 0.05$)

[3] significantly uniform ($P < 0.05$)

Table 6. Size of areas in hectares occupied by adult and juvenile malé spruce grouse in 1974 and 1975.

Male no.	Age	Year	Winter Area N	Early Spring Area N	Late Spring Area N
4	Ad.	1975			1.0(17)
5					1.9(14)
6					0.8(11)
7					0.3(12)
17			2.1(25)		
		$\bar{x}$±SD			1.0±0.7
10	Juv.	1975	14.7(29)	54.3(35)	10.5(19)
11				10.0(31)	
12			7.6(24)	47.0(35)	6.6(20)
14			2.8(22)		
15			1.9(35)	28.5(34)	
22				58.4(24)	2.3(26)
26					14.8(22)
		$\bar{x}$±SD	6.8±5.8	39.6±20	8.6±5.3
27	Ad.	1974			1.8(32)
28					0.5(13)

continued...

Table 6. continued

Male no.	Age	Year	Winter	Early Spring	Late Spring
32					0.7(21)
33					0.7(22)
34					0.9(20)
		$\bar{x}$±SD			0.9±0.5

similar (86 m and 79 m, respectively, Table 7). Male grouse were located in the same tree or clump of trees on consecutive days although not as frequently as females.

Early Spring

Juvenile males greatly expanded areas used during early spring; these overlapped areas occupied by several resident adult males (Figs. 17 and 18). The dispersion of males in section A (Fig. 17) was random (R = 0.84, Table 5); in section B (Fig. 18) too few sightings were made of most individuals to permit calculation of a distribution pattern. Locations of adult males were not individually plotted in Fig. 17 as too few locations were obtained. However, based on the few locations recorded, the areas used were essentially the same as in winter. The two resident adult males in section B also occupied areas similar to those in winter (males 16 and 17, Figs. 16 and 18).

The extensive movements of juvenile males were reflected in the size of areas occupied and the length of daily movements. Average size of areas used was 39.6 ha (Table 6) and daily movements averaged 284 m (Table 7). Mean daily movements of adult males were significantly less than juveniles (Table 7) in both 1974 and 1975. In 1974 adult males moved significantly less than adult males in 1975 (Table 7), possibly influenced by the relative absence of juvenile males in section B in 1974; adult males might move over greater distances if interactions with juvenile males occur frequently when territories are being established.

Figure 17. Spatial relationships among seven juvenile male spruce grouse during the early spring season in section A (April 12 - May 15, 1975).


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Figure 18. Spatial relationships among seven male spruce during the early spring season in section B (April 12 - May 22, 1975). Males 16, 17, 23 and 24 are adults.

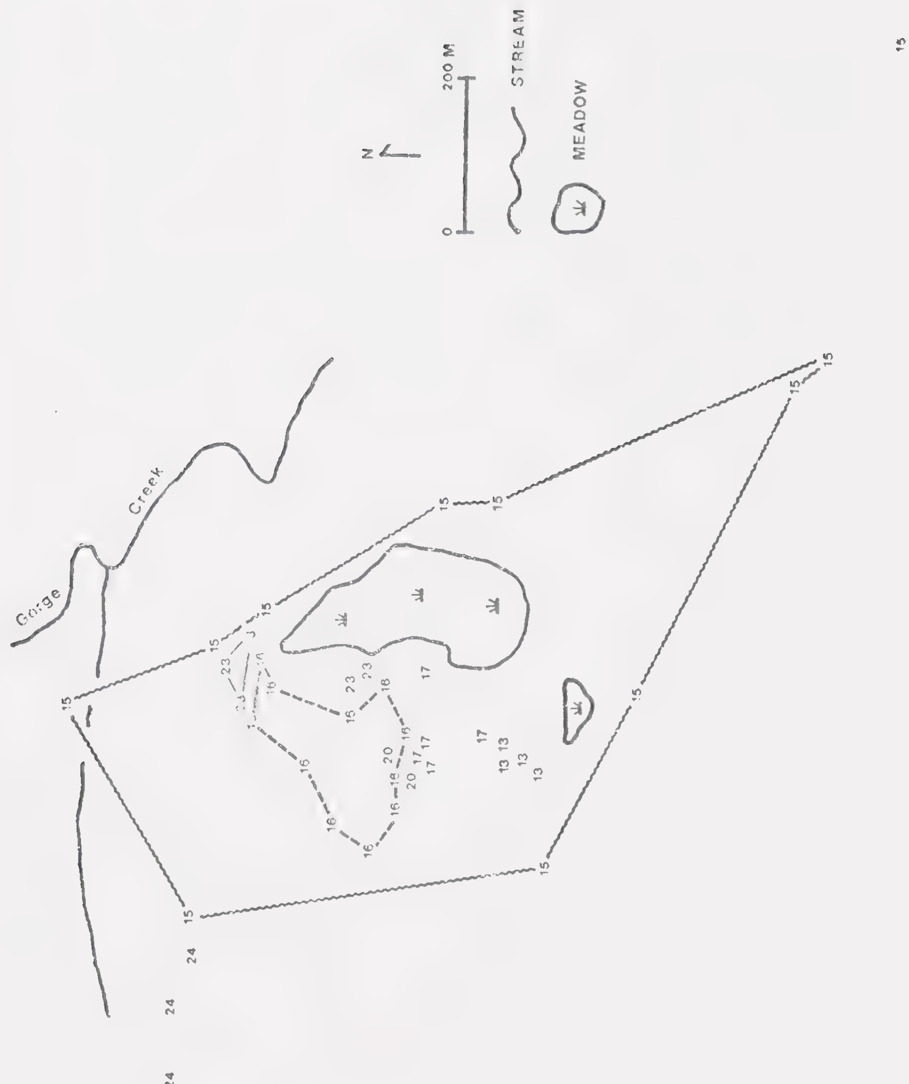
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Table 7. Mean ($\bar{x}$) daily movements in meters of adult and juvenile male spruce grouse in each season of 1974 and 1975.

Age	Year	Winter			Early Spring			Late Spring		
		$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Ad.	1974		-		72	73	32	71	73	8
Ad.	1975	86	81	28	130	71	19	68	26	7
Juv.	1975	79	112	86	284	321	139	334	266	79

Late Spring

Adult male spruce grouse maintained well-defined territories during late spring (Figs. 19 and 20). Overwintering juvenile males 11 and 21 established territories in section A and restricted their activities to small areas. The dispersion of territorial males was uniform (R = 1.93, Fig. 19 and R = 1.6, Fig. 20, Table 5). Average territory size of adult males was 1.0 ha (Table 6); few locations were obtained for juvenile males 11 and 21 (male 11 died on May 22 and male 21 was not radio-tagged) but areas used by both males appeared similar to those of adult males. Mean daily movements were similar for adults in both years (71 m, 1974 and 68 m, 1975, Table 7).

Two overwintering juvenile males (12 and 22, Fig. 19) used areas of 6.6 and 2.3 ha but neither were observed to display within these areas. Juvenile male 10 used an area of 10.5 ha (Fig. 19) before finally departing on May 25 but was rarely seen to display. Male 26 immigrated onto the study area on May 11 and moved over a large area (14.8 ha, Table 6). These four males did not respond when tested with a recording of female calls and were located only peripherally to the territories of displaying males (Fig. 19). Mean daily movements of displaying males were significantly less ($P<0.01$) than those of non-displaying juveniles (Table 7). The dispersion of all males in section A was random (R = 0.96, Table 5).

Summer and Autumn

Male spruce grouse displayed with less intensity as females began to incubate and by mid-June they began to move outside late-spring

Figure 19. Spatial relationships among 11 male spruce grouse during the late spring season in section A (May 16 - June 9, 1975); early spring sightings of adult males also included. Males 4-8 and 25 are adults.


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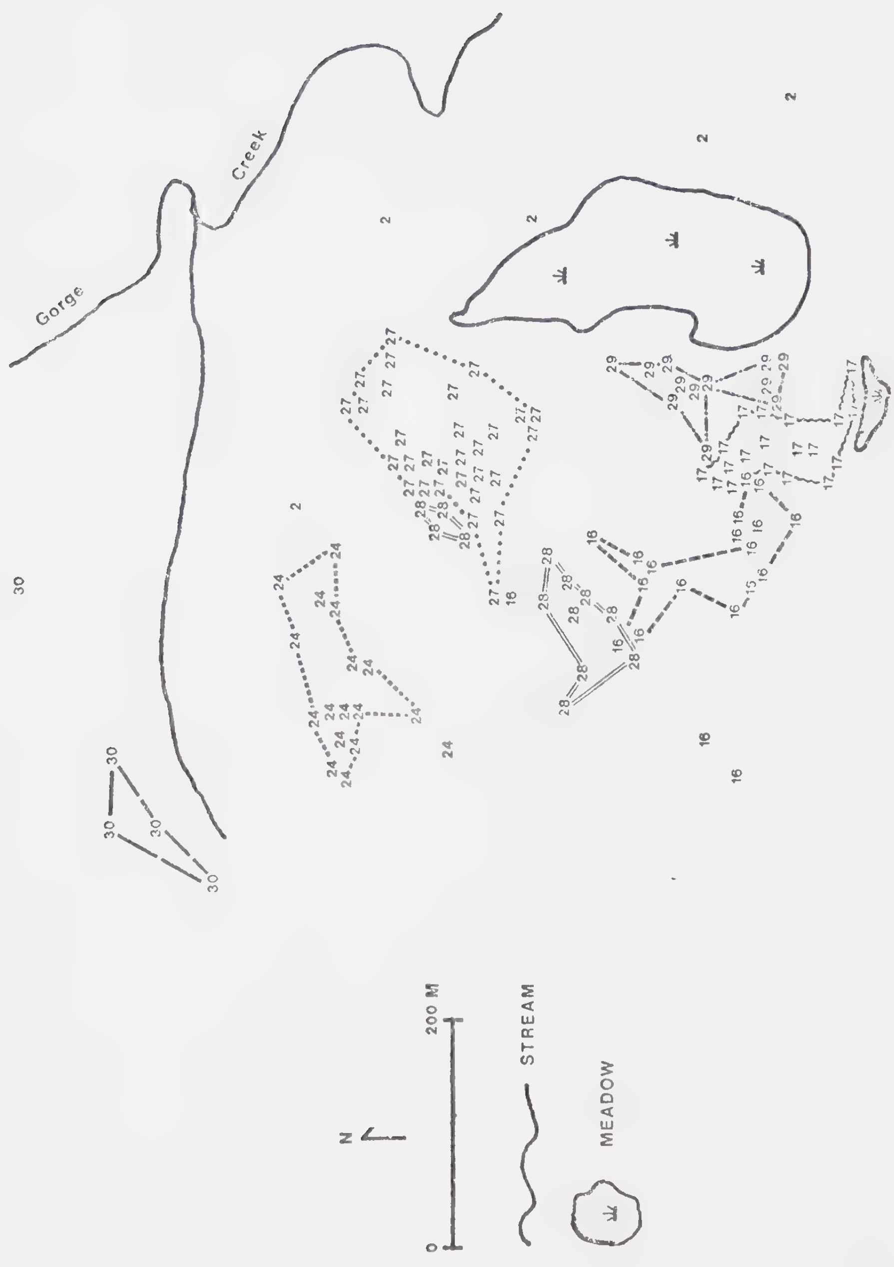
Figure 20. Spatial relationships among eight male spruce grouse during the early and late spring seasons in section B, 1974 (April 9 - June 7, 1974). Males 16, 17, 24, 27, 28, 29 and 30 are adults.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territories. Specific attempts were not made to locate males during summer. Occasional sightings of territorial males were often far from areas known to be used in spring; non-territorial juvenile males also were located outside areas used in spring.

In late summer and early fall a resurgence of display activity occurred. Banded territorial males were located in basically the same areas that they occupied the previous spring. No quantitative data are presented on these phases of male activity because of small sample sizes.

Behavior of Female Spruce Grouse

The tape recording of female calls was played to individual female spruce grouse to determine their behavioral responses over time and to determine whether this behavior might be related to the type of dispersion observed. The reactions obtained from juvenile and adult females during the early and late spring seasons in 1974 are presented in Table 8. Adult females 19 and 22 responded by answering the call and approaching the recorder when first tested on April 23 and 27. Female 18 was a migratory adult known to be on winter range; she did not call or react overtly to the playback. Female 21 did not call until May 26 and was the only resident adult female that did not call in response to the recording during earlier testing (Table 8).

Female 22 failed to call in response to the playback on May 25 and June 5 after calling strongly five times from April 23 to May 12. However, on May 25 she did call in response to the call of a neighboring female that had called in response to the tape. It appears the failure of female 22 to call on these later dates may have been due to an habituation to the recording. Female 23 arrived on the area as a spring resident on May 6 and called when first tested on May 8.

None of the three overwintering juvenile females tested called in response to the recording and each fled from the test site on one occasion (females 26, 27 and 28, Table 8). All three of these juveniles left the study area during spring dispersal. The two juvenile females that immigrated to the study area called when tested within the areas where they became established (Table 8). Female 11 was not tested until her movements indicated a strong degree of localization and female 39 was observed for the first time when she responded to the recording while

Table 8. Overt response of adult and juvenile female spruce grouse to a playback of a tape recording of female calls in 1974.

		Season																					
		Early Spring																Late Spring					
		April					May													June			
Female no.	Age	19	23	27	29	30	5	6	8	9	12	17	18	22	23	24	25	26	30	1	6	8	9
17	Ad.												+*		+								
18			-		-																		
19				+	+				+			+					+			+*			+
20												+							+*			+*	
21		-	-		-							-						+*		+*			
22			+*		+*			+*	+*		+*						-				-		
23									+						+								
26	Juv.					-			-	-°													
27		-	-°		-								-										
28		-	-		-		-°	-															
11																+*			+*				
39																						+*	

\+ Positive overt response involving calls

+* Positive overt response involving calls and approach

\- No overt response

-° Negative overt response with bird fleeing the test site

it was being used to test another female.

The intiation of field work in mid-winter of 1975 and the addition of new sections in the study area provided an opportunity to conduct experiments over a longer time span with more individuals than in 1974, particularly with juvenile females. Experiments were conducted from March 4 until June 4 and were resumed again during the autumn season. The same response pattern obtained in 1974 was evident in juvenile and adult females tested in 1975 (Table 9).

All resident adult females called in response to the recording beginning in early March and continued through May. Overwintering migratory adult females (4, 13 and 55) did not call in response to the playback in March and April while on their winter range (Table 9). However, all three females did react strongly after migration in May.

Overwintering juveniles failed to manifest any responses throughout March and April (Table 9). The two juvenile females (6 and 12) using areas in late spring that included parts of their winter areas began calling when tested on May 10. This coincided with the first departure from the study area of juveniles during spring dispersal. Female immigrants onto the study area (31, 32, 34, 35 and 36) and overwintering juveniles that were followed during spring dispersal until subsequent establishment on breeding range (7, 8 and 56) also reacted in response to the tape recording when tested in late May and early June (Table 9). Unlike resident adult females that called in response to the test recording as early as mid-winter, juvenile females did not respond until late spring at which time they were occupying their future breeding areas. Thus all females present in an area in late spring reacted overtly to the recording which coincides with the season of maximum dispersion (Table 1).

Table 9. Overt response of adult and juvenile female spruce grouse to a playback of a tape recording of female calls.

		Season																			
		Winter								E. Spring					L. Spring						
		March						April				May									June
Female No.	Age	4	8	15	17	19	27	2	5	18	28	10	13	14	16	17	19	21	22	28	4
1	Ad.				+*			+*								+*					
2						+*												+*			
3										+				+*							
4										–										+*	
11		+							+			+*									
13		–							–											+*	
41							+			+					+*						
42							+			+					+*						
55							–		–											+*	
5	Juv.			–				–			–						+*				
6		–	–					–				+*									
7			–					–												+*	

continued...

Table 9, continued...

Female no.	Age	4	8	15	17	19	27	2	5	18	28	10	13	14	16	17	19	21	22	28	4
8			–					–			–										+*
9										–	–										
10		–		–				–					–°								
12		–							–			+*							+*		
14		–							–										+*		
34																		+*		+	
35																				+*	
36																			+*		
31																			+*		
32																					
43							–			–		+									
56																					+*
57							–			–		+*									

\+ Positive overt response involving calls

+* Positive overt response involving calls and approach

\- No overt response

–° Negative overt response with bird fleeing the test site

Adult females were first tested during the fall period on September 8. All individuals responded by calling, but none approached the recorder. Calling was erratic and of low intensity. During three experiments male spruce grouse arrived at the test site and their initiation of courtship activities caused the females to cease calling and leave the site pursued by the males. The arrival of males during other seasons did not prohibit females from continuing to call. Three adults were tested again in late October but failed to respond overtly at that time. Female immigrants tested in late October did not respond to the tape recording. The responses of females to the recording during autumn were in direct contrast to late spring behavior and there appeared to be no attempt by adults or juveniles to prevent immigrants from settling in occupied area.

Opportunities to witness natural encounters between individual females were rare. Calling was seldom heard and female grouse were usually found alone once the late spring period began. On three separate occasions females were observed calling while chasing another female. In all instances the individual calling was clearly the dominant bird as the female being chased did not call back and moved away when the calling bird approached to within approximately 5 - 10 m. Encounters occurred at the end of the early spring season and at the beginning of the late spring season. During the former period one encounter involved two immigrant juvenile females and another an overwintering migratory adult and an overwintering juvenile female. In the first case the dominant immigrant continued to use the area where the encounter was observed; in the second, the overwintering juvenile was the dominant individual and the encounter occurred on the migratory female's winter range just prior to her departure. Unfortunately this juvenile was not observed again after this date and her fate was unknown. The third encounter involved a

resident adult and an immigrant female and occurred within the area used in late spring by the resident adult female. The resident female was clearly the dominant individual and nearly physically attacked the immigrant female before the latter fled from the area. These observations together with the results of the playback experiments appear to indicate that behavioral interactions may be an important mechanism in determining the spatial relationships of individuals.

DISCUSSION

The results of this study indicate that spruce grouse occupy areas that are uniformly spaced during late spring. Not all birds entering this population in late spring were breeders (e.g. non-displaying juvenile males and possibly some juvenile females) and not all areas occupied were indeed exclusive - non-territorial juvenile males overlapped females of both age-classes. All birds actively involved in reproduction occupied areas that were exclusive of other reproducing individuals (particularly those of the same sex) but not necessarily of all members of the spring resident population.

Exclusive areas occupied by female spruce grouse are uniformly distributed throughout suitable habitat and tended to be located around the periphery of a central core of territorial males. The mechanism for maintaining spatial separation between individual females appears to be behavioral; resident adult females are aggressive toward one another and toward juvenile females attempting to settle in the same habitat. Juvenile females also interact aggressively with one another when attempting to establish breeding ranges in late spring. Most adult females are located in late winter close to their subsequent late-spring areas. Positive overt responses of these females to tape-recorded calls at this time appear to indicate firm site attachment to these areas although adults were found with juvenile females and no overt hostility was observed. Migratory females which do not engage in reproductive activities on their winter areas did not respond aggressively to the tape-recorded calls but did so on their breeding areas. Thus behavioral responses are associated with occupancy of a breeding area.

Hostile encounters between individual females were not observed until early May. These coincided with spring dispersal of overwintered

juveniles at which time juveniles were responding aggressively to the tape-recorded calls for the first time. At this time adult females were beginning to maintain exclusive areas and those juvenile females which successfully entered the resident population also established exclusive areas. As encounters were rarely observed and calling seldom heard, areas may be maintained by mutual avoidance rather than overt hostility. These exclusive areas can be termed territories following both Noble's (1930) definition of territory as a "defended area" and Pitelka's (1959) concept of territory which stresses exclusive use of resources and dispersion of members of the population. The long daily movements of both juvenile and adult females recorded during this season may reflect patrolling activities necessary to maintain territorial integrity. Definitive territorial boundaries were not observed.

Areas occupied by female spruce grouse during all other seasons (winter, early spring, summer and autumn) would appear to be best described as home ranges (Burt 1943). These areas are not known to be defended and often considerably overlap one another. Females with broods travel extensively over large areas as reported by Ellison (1973) and Haas (1974). Unlike Ellison (1973), I observed no long distance movements (2-3 km) of females with broods although Keppie (1975) observed new broods entering the study area in late summer which may have moved long distances. Females were rarely located in close proximity to one another during summer; spatial separation seemed to be temporally maintained.

What is the selective advantage of female territoriality during late spring? Is the pattern of spacing related to the amount or quality of food? Although sampling was not intensive during the late spring season (birds were collected on May 11 and June 10), Pendergast and Boag (1970) indicated spruce grouse began to select newly sprouting herbs as they

became available with a corresponding decrease in the use of conifer browse. I observed female spruce grouse feeding on herbaceous vegetation during late spring on several occasions. This food resource may not be readily available as new growth is just beginning to appear. Thus the possibility exists that female spruce grouse establish territories to protect a rare food source for themselves during the prelaying period. Long daily movements recorded at this time may also be in search of newly sprouting herbs. Female red grouse (*Lagopus lagopus scoticus*) require a high-nutrient diet for egg production, hatching success and subsequent survival of chicks (Miller *et al.* 1966, Moss 1968). Thus female spruce grouse that obtain a nutritious food source during prelaying (herbs or conifer browse) would increase their chances of breeding success and survival of their offspring.

Another possibility involving the food resource concerns the diet of female spruce grouse during incubation. Females appear to select the growing tips of needles of white spruce (*Picea glauca*) throughout incubation (Pendergast and Boag 1970 and Herzog, unpubl. data). Spruce needles and new leaders are bulky and can be obtained easily allowing incubating females to feed quickly and may be digested more slowly than herbs during long periods of incubation between feeding trips. Females would also leave less scent for predators to find by feeding in trees rather than walking to acquire herbs. On one occasion I followed a female to a feeding tree she used frequently in which another female was already present. After feeding for 20 to 30 seconds the female that I had followed called twice and the other female (an immigrant juvenile that was not incubating) flew from the tree out of sight. This female may have left because of the call or because she was satiated and had ceased to feed. The female call was played to five females during their incubation periods

while feeding in spruce trees and in each case they called in response; in one instance the female flew to the ground and approached the recorder. These females may have been responding to the call to defend the feeding site or their territory as a whole. However, these observations suggest that female spruce grouse may establish exclusive areas to ensure adequate food resources during incubation. Many authors have considered the role of food in the establishment of territorial systems (Hinde 1956, Tinbergen 1957, Wynne-Edwards 1962, Brown 1969 and others) and Lack (1954, 1966) felt that the distribution of essential resources (mainly food) was the primary cause of spacing. The relationship of food resources and female territoriality is certainly an area for future research.

The uniform distribution of female spruce grouse in late spring ensures a wide dispersion of nests and may reduce the chances of nest predation. This is of direct survival value to potential offspring and females themselves may be less vulnerable to attack when nesting alone. Females do not nest on male territories possibly because male display sounds attract predators. If dispersion is more efficient than aggregation (flocking) as a means of increasing survival and production, spacing behavior may have evolved primarily to reduce predation with food selection in late spring basically a matter of preference rather than need.

The mechanisms and consequences of female spruce grouse territoriality may apply to other species of forest grouse, an area that needs to be investigated. Stirling (1968) observed aggressive behavior of female blue grouse in the aviary and suggested this behavior may occur in the field to space females and Zwickel (1973) felt that behavioral interaction might space female blue grouse during the brood season. Boag (1966) and Bendell and Elliot (1967) observed extensive overlap of female blue grouse home

ranges in spring although the latter believed individual birds were evenly spaced. However, in these studies observations of individuals were infrequent and it is doubtful occasional sightings of banded individuals would reveal a system of territoriality of three to four weeks duration if it exists. Brander (1967) radio-tracked female ruffed grouse and their movements indicated an attraction to areas occupied by drumming males but spatial relationships are unknown. Intensive radio-telemetry studies in suitable areas with a workable density of birds would indicate to what extent females of these two species are interacting in spring. The need to capture all females in a particular study area is a major difficulty in such a field project.

Territoriality of male spruce grouse recorded in this study was similar to that described by Stoneberg (1967), McLachlin (1970), Ellison (1971, 1973) and Anderson (1973) although in this study juvenile males which did not display on small territories, nevertheless, occupied fairly exclusive areas, peripheral to the aggregated territorial males but overlapping female areas. These juvenile males did not respond with display activity to tape-recorded female calls as did territorial males and I never observed these males performing flutter flights or wing-clapping (MacDonald 1968). Observations of these males were limited to brief encounters and may not accurately represent their degree of display activity. These juvenile males, unlike those studied by Ellison (1971), ceased to make long excursions from their main areas of use during the period of intense late spring display, although these excursions occurred regularly during the early spring period. Long daily movements during the late spring season were confined to discrete ranges and may reflect attempts to maintain exclusive areas.

The aggregation of territorial male spruce grouse that I observed

in this study is similar in density and spacing to that of male capercaillae (*Tetrao urogallus*) (Hjorth 1970) and I believe this association may be termed an arena. Individual male spruce grouse react to the display sounds of their neighbors with flutter flights and wing-claps (MacDonald 1968) and during intense display several males can be heard from one point. Such clumping of territorial male spruce may only occur when densities of birds are high, as suggested by Gullion (1976) for ruffed grouse as he considers habitat selection to be a stronger influence than social interaction in clumping of drumming males. Although further research is needed on this point, my impressions of the forest habitat lead me to believe that social interaction may be a stronger force in clumping males than habitat considerations as the display sites of males are not particularly unique and males will shift territories from year to year. These shifts may be influenced by loss of neighbors. The extent to which food resources play a role in male territoriality is unknown but the main function of this system may be to facilitate mating as copulations are unlikely to be interrupted by neighboring males and females may be able to locate a group of displaying birds more easily than solitary individuals when they are ready to mate.

The territorial systems of both sexes of spruce grouse may influence the recruitment of juvenile birds to the spring resident population. Keppie (1975) documented spring dispersal of juvenile birds from this same population from early March to mid-May with most birds being lost (failure to sight banded individuals) after April 1. Males appeared to leave earlier than females and the loss of overwintered juveniles occurred prior to the arrival of new birds on the study area (Keppie 1975). Emigration and immigration of juvenile birds coincided in this study and the possibility exists that the banded birds missing early in Keppie's (1975) study had not

actually left the study area but were not observed because they were more mobile at this time. Juvenile males appeared to wander earlier than juvenile females in my study possibly because of the earlier onset of male territoriality.

Keppie (1975) stated that spring dispersal was an important means of adjusting numbers of birds in the spring resident population but felt it was not the basic mechanism involved as something must stimulate birds to move. I believe the stimulus is behavioral and that the same mechanism (aggressive behavior) spaces birds on the breeding range and also forces juvenile birds out of the population during spring dispersal. Overwintered juveniles of both sexes begin to move extensively in early spring, possibly in search of suitable unoccupied breeding areas or in attempts to avoid areas occupied by residents. Those juveniles that establish territories in their winter ranges may be more aggressive in interactions between themselves and resident adults; those unable to acquire such an area may be forced out of the population and so disperse. Immigrant juveniles may arrive in a particular area later in the season and may be more aggressive than emigrants, or resident birds may become more tolerant. Most spring emigrants survive into the summer (Keppie 1975) in habitat outside the study area. Keppie (1975) removed all the adult birds from a section of the study area in late winter to test the hypothesis that adult birds were influencing the dispersal of juvenile birds. The rate of dispersal was similar on the removal and control areas which appears to negate the influence of adult birds. However, the removal area was small (60 ha) and the total number of birds breeding in the area was the same as the previous year. The possibility certainly exists that juveniles were interacting with one another with less aggressive individuals moving out of the study area. There may also be an attraction of juvenile birds (especially males) to areas occupied

by adults. A removal experiment (complete removal of adults in early winter) conducted over a large area (150 ha) with intensive radio-tracking of remaining juveniles would give better insight into the influence of adult birds on spring dispersal.

If the territorial behavior of adult spruce grouse is important in influencing the rate of spring dispersal and recruitment of juveniles, to what extent is such behavior important in the regulation of breeding numbers? Lack (1954, 1966) believed that in nearly all instances territorial behavior serves only to space individuals after their numbers have been determined by other factors (mainly starvation). Tinbergen (1957) and Wynne-Edwards (1962) believed that territorial behavior can limit numbers and studies by Watson (1967), Harris (1970), and Krebs (1971) support this idea. Watson and Moss (1970) felt social behavior could limit numbers only when certain conditions are fulfilled and it is useful to compare the available evidence concerning spruce grouse with these conditions. The first and critical condition of Watson and Moss (1970) is that a substantial portion of the study area bird population does not breed as a result of the social behavior of other members. Most spruce grouse in the resident population studied apparently bred, with the possible exception of those juvenile males which do not display regularly and a few immigrant juvenile females for which no evidence of nesting activity was obtained. Most emigrants survive (Keppie 1975) and three juvenile females radio-tracked during spring dispersal in my study nested which provides evidence that socially-induced mortality as a result of emigration may be uncommon. Thus social behavior of spruce grouse does not appear capable of limiting numbers under the conditions of Watson and Moss (1970).

Territorial behavior may be influential in determining the density of the breeding population in preferred habitats (Kluvyer and Tinbergen

1953) and this may be the situation observed in this study. That the study area is preferred habitat is substantiated by the fact that spruce grouse are present in the highest density reported in the literature and that censuses in areas near the Gorge Creek study area indicate lower densities of birds (D. Keppie, personal communication). Brown (1969) listed three levels in relating territorial behavior and its possible influence on breeding density. I believe level 2 closely coincides with the results of this study and Keppie's (1975): "some individuals become dissuaded from breeding in the preferred habitat by the territorial behavior of the birds already established there: but these birds typically breed in other, less productive habitats (Brown 1969: 294). How immigrant juveniles are able to establish breeding areas in habitat left by over-wintered juveniles is a question that deserves future attention.

Until more evidence is available, the territorial behavior of spruce grouse appears to be either a response to competition for ecological requirements (food or breeding space) and/or the result of the evolution of an anti-predator mechanism. Secondarily this behavior serves as a mechanism for adjusting breeding density through spring dispersal of juvenile birds. Bendell *et al.* (1972) and Zwickel (1972) suggest that regulation of numbers of blue grouse involves behavioral interactions between resident adults and juveniles during spring and this interaction may indeed be similar to the behavior of spruce grouse observed in this study.

BIBLIOGRAPHY

ANJE, B. 1968. A simple test for uniformity of a circular distribution. Biometrika 55:343-354.

ANDERSON, L. J. 1973. Habitat use, behavior, territoriality, and movements of the male spruce grouse of northern Minnesota. M.S. Thesis. University of Minnesota, St. Paul. 119 pp.

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Amer. Inst. Biol. Sci. Monogr. 57 pp.

BENDELL, J.F., and P.W. ELLIOT. 1967. Behaviour and the regulation of numbers in blue grouse. Can. Wildl. Serv. Rep. Ser. 4. 76 pp.

__________, D. G. KING, and D. H. MOSSOP. 1972. Removal and repopulation of blue grouse in a declining population. J. Wildl. Manage. 36(4): 1153-1165.

BERNDT, R., and H. STERNBERG. 1968. Terms, studies, and experiments on the problems of bird dispersion. Ibis 110:256-259.

BOAG, D.A. 1966. Population attributes of blue grouse in southwestern Alberta. Can. J. Zool. 44(5):799-814.

BRANDER, R. B. 1967. Movements of female ruffed grouse during the mating season. Wilson Bull. 79(1):28-36.

__________. 1968. A radio-package harness for game birds. J. Wildl. Manage. 32(3):630-532.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81(3):293-329.

__________, and G. H. ORIANS. 1970. Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. 1:239-262.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24(3):346-353.

CLARK, P. J., and F. C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35(4):445-453.

DUMKE, R. T., and C. M. PILS. 1973. Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. Wisconsin Dept. Nat. Res. Tech. Bull. No. 72. 52 pp.

ELLISON, L. N. 1971. Territoriality in Alaskan spruce grouse. Auk 88(3):652-664.

__________. 1973. Seasonal social organization and movements of spruce grouse. Condor 75(4):375-385.

GULLION, G. W. 1976. Reevaluation of "activity clustering" by male grouse. Auk 93(1):192-193.

HAAS, G. H. 1974. Habitat selection, reproduction, and movements in female spruce grouse. Ph.D. Thesis. Univ. of Minnesota, St. Paul. 124 pp.

HARRIS, M. P. 1970. Territory limiting the size of the breeding population of the oystercatcher - a removal experiment. J. Anim. Ecol. 39(4):707-713.

HARVEY, M. J., and R. W. BARBOUR. 1965. Home range of *Microtus orchrogaster* as determined by a modified minimum area method. J. Mammal. 46(3):398-402.

HINDE, R. A. 1956. The biological significance of the territories of birds. Ibis 98:340-369.

HJORTH, I. 1970. Reproductive behavior in Tetraonidae. Viltrevy 7(4):1-596.

KEPPIE, D. M. 1975. Dispersal, overwinter mortality, and population size of spruce grouse. Ph.D. Thesis. Univ. of Alberta, Edmonton. 113 pp.

KLUVYER, H. N., and L. TINBERGEN. 1953. Territory and the regulation of density in titmice. Arch. Neerl. Zool. 10:265-286.

KREBS, J. R. 1971 Territory and breeding density in the great tit. Ecology 52(1):2-22.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 pp.

__________. 1966. Population studies of birds. Clarendon Press, Oxford. 341 pp.

LANCE, A. N. 1970. Movements of blue grouse on the summer range. Condor 72(4):437-444.

LUMSDEN, H. G. 1961. Displays of the spruce grouse. Can. Field. Nat. 75(3):152-160.

MACDONALD, S. D. 1968. The courtship and territorial behavior of Franklin's race of the spruce grouse. The Living Bird 7:5-25.

MCCOURT, K. H. 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in southwestern Alberta. M.S. Thesis. Univ. of Alberta, Edmonton. 137 pp.

MCLACHLIN, R. A. 1970. The spring and summer dispersion of male Franklin's grouse in a lodgepole pine forest in southwestern Alberta. M.S. Thesis. Univ. of Alberta, Edmonton. 153 pp.

MILLER, G. R., D. JENKINS, and A. WATSON. 1966. Heather performance and red grouse populations. I. Visual estimates of heather performance. J. App. Ecol. 3:313-326.

MOSS, R. 1969. A comparison of red grouse stocks with the production and nutritive value of heather. J. Anim. Ecol. 38(1):102-112.

NOBLE, G. K. 1939. The role of dominance in the social life of birds. Auk 56(3):263-273.

ODUM, E. P., and E. J. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72(2):128-137.

PENDERGAST, B. A., and D. A. BOAG. 1970. Seasonal changes in diet of the spruce grouse in central Alberta. J. Wildl. Manage. 34(3):605-611.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. Condor 61(2):233-264.

ROBEL, R. J., J. N. BRIGGS, J. J. CEBULA, N. J. SILVY, C. E. VIERS, and P. G. WATT. 1970. Greater prairie chicken ranges, movements and habitat usage in Kansas. J. Wildl. Manage. 34(2):286-306.

STEEL, R. G. D., and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., Toronto. 481 pp.

STIRLING, I. 1968. Aggressive behavior and the dispersion of female blue grouse. Can. J. Zool. 46(3):405-408.

STONEBERG, R. P. 1967. A preliminary study of the breeding biology of the spruce grouse in northeastern montana. M.S. Thesis. Univ. of Montana, Missoula. 82 pp.

TINBERGEN, N. 1957. The functions of territory. Bird Study 4(1):14-27.

WALLESTAD, R., and D. B. PYRAH. 1974. Movements and nesting requirements of sage grouse hens in central Montana. J. Wildl. Manage. 38(4):630-633.

WATSON, A. 1967. Population control by territorial behavior in red grouse. Nature 215:1274-1275.

__________, and R. MOSS. 1970. Dominance, spacing behavior, and aggression in relation to population limitation in vertebrates. Pages 167-220 *In* A. WATSON, ed. Animal populations in relation to their food

resources. Blackwell Scientific Publications, Oxford. 477 pp.

WILEY, R. H. 1974. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49:201-227.

WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh. 653 pp.

ZWICKEL, F. C., and J. F. BENDELL. 1967. A snare for capturing blue grouse. J. Wildl. Manage. 31(1):202-204.

__________. 1972. Removal and repopulation of blue grouse in an increasing population. J. Wildl. Manage. 36(4):1141-1152.

__________. 1973. Dispersion of female blue grouse during the brood season. Condor 75(1):114-119.

Appendix 1. The range in number of sightings necessary to accurately estimate (95 percent confidence level) the area used by individual grouse during each season.

Sex	Season	Number of sightings
Female	Winter	15 - 25
	Early spring	20 - 25
	Late spring	10 - 15
	Summer	25 - 35
	Autumn	20 - 25
Male	Winter	15 - 25
	Early spring	20 - 25
	Late spring	10 - 15

Appendix 2. Comparison of daily movements between first sightings on consecutive days (a.m. - a.m.), p.m. - a.m. movements on consecutive days, and within day (a.m. - p.m.) movements of female spruce grouse.

		Type of Movement								
		a.m. - a.m.			p.m. - a.m.			a.m. - p.m.		
Season	Age-class	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Early spring	Juvenile	179	215	317	97	183	24	35	45	27
Early spring	Adult	104	100	185	91	111	36	64	58	37
Late spring	Juvenile	234	179	102	99	91	11	47	42	12
Late spring	Adult	140	114	167	118	123	42	102	91	45
Summer	Adult[1]	138	103	434	127	92	7	83	46	8
Summer	Adult[2]	200	126	220	194	111	71	164	101	19

[1] Females without brood

[2] Females with brood

Appendix 3. Daily movements and orientation of juvenile female spruce grouse during spring dispersal and adult female spruce grouse during spring migration.

Spring Dispersal

Bird No.	Day	Distance (km)	Angle of travel (°)	A[1]
7	1	0.5	41	-
	2	0.5	64	
	3	0.8	67	
	4	0.7	58	
	Total distance	2.5	Mean angle 58±12[2]	
			True bearing N58°E	
8	1	0.8	68	400*
	2	1.1	63	
	3	1.2	96	
	4	1.4	103	
	5	1.2	114	
	6	1.1	118	
	Total distance	6.8	Mean angle 94±23[2]	
			True bearing N4°E	
58	1	0.5	48	494*
	2	0.9	70	
	3	2.5	73	
	4	1.7	74	
	5	1.2	74	
	6	1.2	73	
	Total distance	8.0	Mean angle 69±10[2]	
			True bearing N21°E	

Appendix 3. continued.

Spring Migration

Bird No.	Day	Distance (km)	Angle of travel (°)	A[1]
13	1	.7	85	-
	2	2.1	74	
	3	1.8	55	
	4	1.1	53	
	Total distance	5.7	Mean angle 67±15[2]	
			True bearing S67°E	
59	1	.7	59	-
	2	1.2	73	
	3	.7	75	
	Total distance	2.6	Mean angle 69±9[2]	
			True bearing S69°E	

1 Ajne 1968, test for randomness, *direction preferred

2 Batschelet 1965

* $P<0.005$